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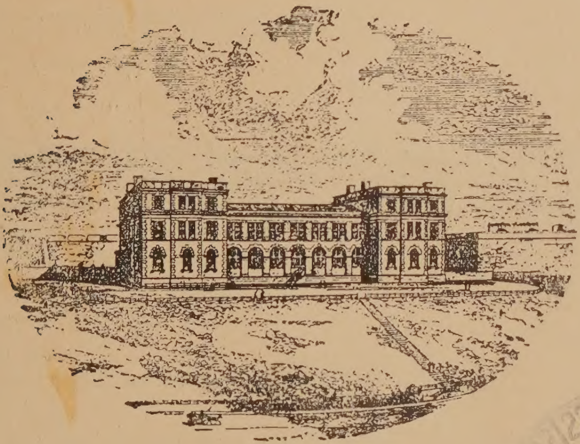

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Studies on Conditioned Responses in Fishes. Part VII.
Temperature Perception in Teleosts.

By
Herbert O. Bull, Ph.D.,
The Dove Marine Laboratory, Armstrong College, University of Durham.

With 3 Figures in the Text.

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INTRODUCTION.

TEMPERATURE plays a large part in regulating the lives of all "cold-blooded" animals. It affects directly their rate of metabolism and their time of reproduction. Such effects are readily shown by *direct* physiological experiments on isolated tissues or organs and by simple observation of total behaviour. As to how far fishes may be supposed to *react purposively* to the temperature changes to which they are constantly subject we have no knowledge.

The present paper describes a series of experiments, using the method of the conditioned response, made with different kinds of fishes to find out whether they react in this way towards, or perceive objectively, small increases in temperature of the water surrounding them. The discussion at the end of the paper shows that a definite answer to this problem is of value in the successful prosecution of certain aspects of fishery research.

The experiments themselves were the first major research undertaken in the sound-insulated building erected for the purpose of these studies on conditioned behaviour. They could not have been carried out satisfactorily under any ordinary laboratory conditions. I wish therefore to record here, particularly, my deep appreciation of the action of H.M. Development Commissioners and of the Council of Armstrong College, University of Durham, in jointly providing this building for my researches. A description of the building is given in Part IV of these studies (1).

Outline of Method.

The general principles involved may be simply stated as follows. A slight increase in temperature of the water flowing past a fish is associated over a period of several weeks with the giving of food at a succeeding constant interval of time. The experiment is designed so that a well-marked motor response necessarily associated with the acquisition of food can be used as the registerable conditioned reaction and hence of discriminatory perception. Special tanks have therefore to be devised, for they have not only to be of such a size and shape as to be satisfactory for the application of a temperature stimulus, but they must also be such in which active fishes will live healthily and, as far as can be judged, "contentedly," for the several months required in coming to a reliable conclusion. The thermal stimulus has to be given in a way which precludes the possible operation of an associated factor as a "signalling" stimulus. It is difficult to do this in a way which will enable one to measure the temperature at the point of stimulation on an actively swimming fish, especially when the observer himself must remain concealed. It cannot be too strongly emphasised that reliable conclusions upon sensory perception in animals are, largely owing perhaps to the interference of unknown stimuli, extremely difficult to obtain.

It may well be that our present knowledge of the relationships between animals and their environment contains many serious misconceptions arising primarily out of these difficulties. It is believed that they have been overcome in the present work.

Apparatus.

Two arrangements were used, one for the larger, mostly free-swimming fishes (I), the other for small, mostly sedentary forms (II). In essentials these were alike, the differences between them being only of degree.

Arrangement I (photograph, Fig. 1 ; plan of arrangement in Fig. 2).

ABC and $A_1B_1C_1$ (fig. 2) are two similar strongly constructed wooden tanks with asphalt lining, 3 metres long, 15 cm. wide, 25 cm. deep, open at the top, and originally designed for a different purpose, but found quite serviceable for these experiments. The side of the one nearest the observer was continued upwards into a board inclined over the tank at 45° to form an effective screen (S_1, fig. 2) between the fish and the observer. The tanks rest in an inclined position on thick pads of felt which reduce sound conduction through the floor to a minimum (this itself was laid specially with the same end in view (see Pt. IV), **1**). By giving the tank this slope from A to C, a graduated depth of water is obtained from nil at A to a few cm. (varied according to species) at C. Sea-water from the Laboratory system enters at A through the tube D (fig. 2). It discharges through a fine jet, flows down the tank, and out to waste at C. The rate of flow was maintained constant for the duration of an experiment. The effect of the graduated depth of water is to limit the normal activities of the experimental fish to that part of the tank where it is covered with water (between B and C) and the depth at C was determined by this factor. This obvious restriction upon the normal activities of the fish decides the course of the experiments and makes it possible to use a simple but very striking conditioned response as evidence of discriminatory perception.

A fish placed in this tank for the first time swims for a while violently up and down, not as a rule passing upwards beyond the centre of the tank (i.e. where it begins to become uncovered). " Excitable " fishes occasionally persist (in those first few minutes) in splashing their way up-stream to the head of the tank in spite of the shallowing water and unless watched will stay there (and possibly die). They do not however attempt to do this after more than one or two such experiences and within a few hours settle down permanently near C. After they have thoroughly settled down, none of the fishes investigated have repeated this violent up-stream splashing or passed the centre of the tank, except for the special circumstances of the experiments as described on pp. 9, 10. It was decided to use this up-stream swimming and splashing response as the conditioned response to be elicited by association with an unconditioned stimulus which would itself evoke this action unconditionally. Considerable patience is needed for the successful conclusion of an experiment and many failures were had in the early stages for reasons which will appear.

Only a very strong incentive will induce a fish to make this difficult up-stream response. This is provided by the introduction of food at the head of the tank. For this purpose, a special food tube enters the outer screen at F. This is arranged so that the observer continues to be hidden from the fish whilst food is given, and so that there are no operations associated with its appearance which are visible to the fish. The tank is divided by a vertical partition (E, fig. 2) 25 cm. from the top end. An opening is cut in this partition so as to form an archway, the small portion AE of the tank constituting the " food chamber." To obtain the food in this chamber the fish must wriggle on its side through the arch, after which, in order to regain its normal position at C, it must either turn completely round in this chamber or go out again backwards, an act which involves much splashing. Even when thoroughly " conditioned " it does this typically with extreme rapidity and nervousness (as if eager to escape from the uncomfortable situation in which it finds itself).

The *temperature* increase which is to serve as the conditioning stimulus is given by the following device. The tube (of Pyrex glass) which carries the sea-water into the head of the tank from the main sea-water supply

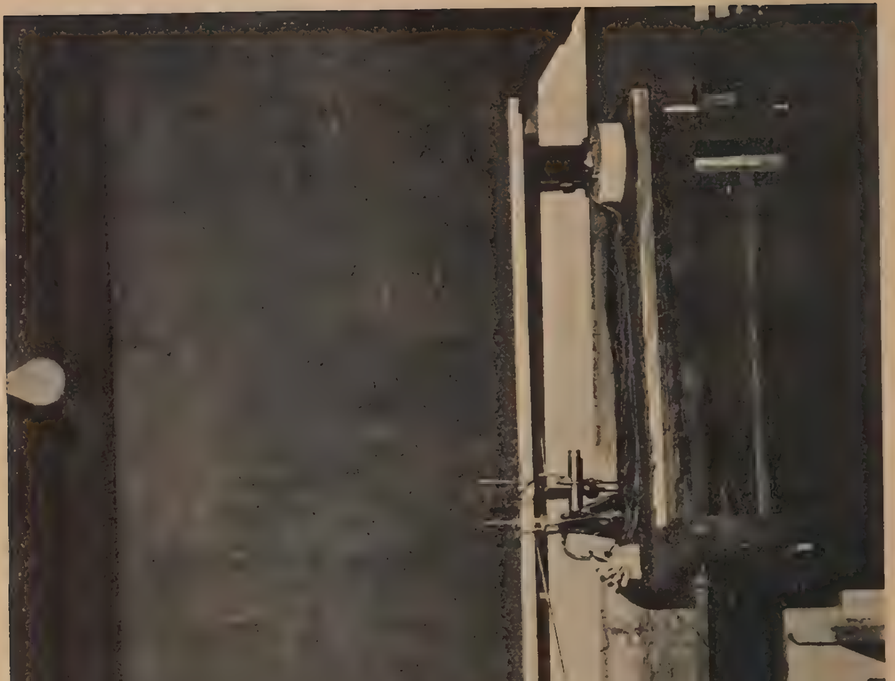

FIG. 1.—Photograph of interior of special building showing the larger tanks (Apparatus I) used in experiments on temperature perception in fishes.

N.B.—The smaller tanks (Apparatus II) were added after this photograph was taken.

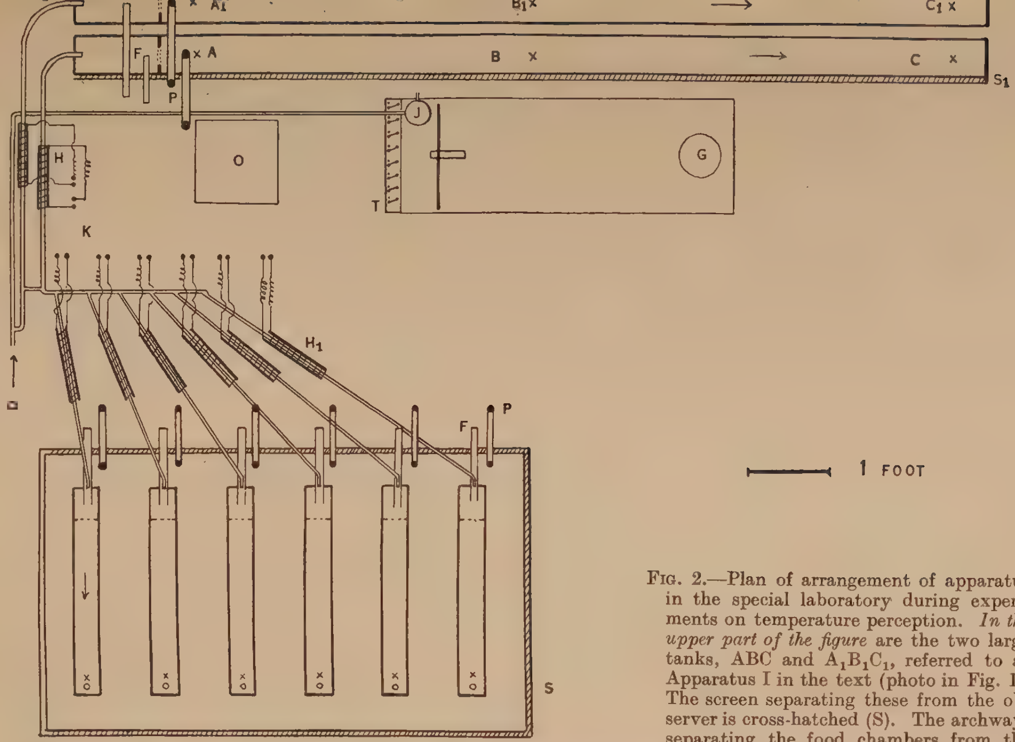

Fig. 2.—Plan of arrangement of apparatus in the special laboratory during experiments on temperature perception. *In the upper part of the figure* are the two large tanks, ABC and $A_1B_1C_1$, referred to as Apparatus I in the text (photo in Fig. 1). The screen separating these from the observer is cross-hatched (S). The archways separating the food chambers from the main bodies of the tanks are labelled E. To the left of these are the food tubes F, and to the right the periscopes for observation (P). Each tank has its separate sea-water supply from D. *In the lower part of the figure* are the six smaller tanks (Apparatus II), enclosed within their common screen S. Each of these is provided with its separate sea-water supply, food tube (F) entering the food compartment, and periscope (P). The taps separating the sea-water supply to each tank are *not* shown: G=mirror galvanometer; H and H1=heating coils (one each for the two large tanks and six small tanks) operated by switches from mains supply; O—observer's seat from which all observations and manipulations can be made; T=Thermo-couple switch board; X="hot-water junctions" of thermo-couples; all the "cold-water junctions" are immersed in J (provided with standard thermometer). The wiring of the thermo-couples is omitted, in order to avoid unnecessarily complicating the diagram. The direction of water flow is shown by arrows.

(D, fig. 2) is wound with a coil of ni-chrome wire (H, fig. 2) connected with the main heating circuit through a soft copper knife switch (K, fig. 2). By closing this circuit for varying lengths of time the water may be heated to varying extents on its passage through the tube into the tank. The heated water then flows down the tank, past the fish, and out to waste. It was found that, as might be expected, the path of this heated water is somewhat complex. This fact itself is not of importance in carrying out the experiments, it being essential to measure only the temperature at the surface of the fish.

For the proper appreciation of the performance of the experiments it is however necessary to outline what takes place at various positions in the tank. It has to be borne in mind that the fish has no restriction placed upon its movements in the tank, other than that effected by the shallowing of the water from C to A. The temperature-recording mechanism must therefore be both easy to move and without any serious time-lag.

For this purpose a system of copper-constantin thermo-couples, used in conjunction with a sensitive mirror galvanometer, were found suitable. The couples were of single strands of No. 34 S.W.G. Constantin and No. 38 S.W.G. copper, the junctions being made with a small bead of silver, using dry borax as flux. Each couple was entirely enclosed in glass tubing to prevent corrosion from the atmosphere which here rapidly attacks unprotected metal. The thermo-couples were thus constant for the duration of the experiments, and no replacements were necessary. The " cold " junction (J, fig. 2) was immersed in a conical flask with side tube through which the same water as that entering the experimental tank constantly circulated; this ensured that this junction was always of the same temperature as the unheated tank water with possibly a very small difference for which the necessary correction could always be applied. At both " hot " and " cold " junctions the enclosing glass tubing was drawn out to a fine point, the end of which was sealed and filled with a small drop of mercury in which the actual junction was immersed. The couples were used in conjunction with an Onwood reflecting moving-coil galvanometer (Gambell Bros., Pattern 3041) used aperiodically. This had a sensitivity at 1-metre scale distance of 130 mm. per micro-amp. with a timing of 7 sec. for a complete swing. With a shunt resistance of 150 ohms, a " null " deflection of approximately 6 mm. was obtained for 0·1° C. variation in temperature. Each thermo-couple was separately calibrated against " A " N.P.L. certified thermometers over the range required and under the exact conditions of the experiment. This was done by attaching the thermometers to the thermo-couples with the bulbs of the thermometers in close contact with the junctions. Galvanometer readings were then taken for the whole range of differences in temperature used in the experiments, i.e. nil to 5·0° C. As only the " rise " in temperature was wanted, no " ice " junction was required. One of the standard thermometers remained in the " cold-water " junction for the duration of the experiments to give the " resting " temperature of the water.

The " hot " junctions of three such couples were placed at various positions along the tank in the median line—one just past the entrance to the food chamber, one in the centre of the tank, and the other as near as possible to the normal resting site of the fish ; another was added if this latter was not fairly definite.

A typical picture of the temperature changes induced in the tank during an associative experiment is shown in Fig. 3, p. 8.

In this figure the data relate to three thermo-couples placed (1) at the entrance to the food chamber, (2) In the centre of the tank, (3) At the deep end of the tank, and usually touching the fish. The junctions are placed at a depth of 1 cm., 3 cm., and 4 cm. respectively at these three points.

A completely different picture is found on the surface of the water.

As the usual position of a fish in the early stages of the experiments is at C, several minutes elapse before the warmed water reaches the fish. The whole of this time provides valuable opportunity for noting " unstimulated " behaviour. It follows that whilst the actual temperature at the moment the heated water first reaches the fish is the only aspect of this factor which is of importance to the experiment, the fish is actually under the influence of a much higher temperature for a further and subsequent period of up to nearly fifteen minutes, during which the reactions described later (p. 9) are carried out. The conditioning temperature stimulus acts continually, therefore, up to the completion of the reactions involved in food getting. It may further happen that by the time the fish actually fetches the food in the food chamber the temperature at that point is back to normal, whilst that at the lower end still remains high. In later stages of conditioning the fish not infrequently comes to take up a resting position much higher up the tank, and may acquire a habit of resting as high up as the centre of the tank adjacent to the thermo-couple at B.

Arrangement II (lower portion of fig. 2).

A modification of arrangement I was used for smaller fishes, but in all that has been said in regard to observation and temperature measurement it was essentially the same. Instead of the large wooden type of tank, a small shallow oblong zinc trough (80 cm. long × 11·5 cm. wide) was used. This was similarly inclined to give a graduated depth of water as in the larger tank. It had, in addition, an L-shaped end (omitted in the diagram), but this was a feature introduced primarily for another purpose, and of no material importance in the present series of experiments. Its presence may be entirely disregarded. The normal sea-water entered at the head of the tank, flowed along the length of the tank, becoming deeper on its way, and out to waste at the deep end. In this smaller type of tank all the fishes used took up permanent positions close to the exit so that only one thermo-couple was required. For sedentary fishes such as *Blennius pholis* this was placed so that the fish naturally rested as a rule with its head in contact with the junction. The difficulty of measuring the precise temperature at the point of stimulation was therefore much less in this arrangement than in the larger. As in arrangement I food was introduced into the shallow water through special tubes (F, fig. 2) into a separate food chamber. It was found possible to carry out six experiments simultaneously in six separate tanks of this type owing to their smaller size. All were enclosed in one common surrounding screen, 6 ft. high, and observations made with periscopes of the pattern described in part VI (2). The thermo-couples from all these tanks and the two larger tanks were all immersed at their " cold-water " junctions in the same vessel. They were connected up to the same galvanometer, their circuits being interrupted by knife switches arranged on the galvanometer table at a point convenient for the experimenter who carries out all manipulations and observations whilst seated as quietly as possible in one position where all the eight periscopes can be viewed, food given in any of the eight tubes, and the galvanometer scale read without change in position.

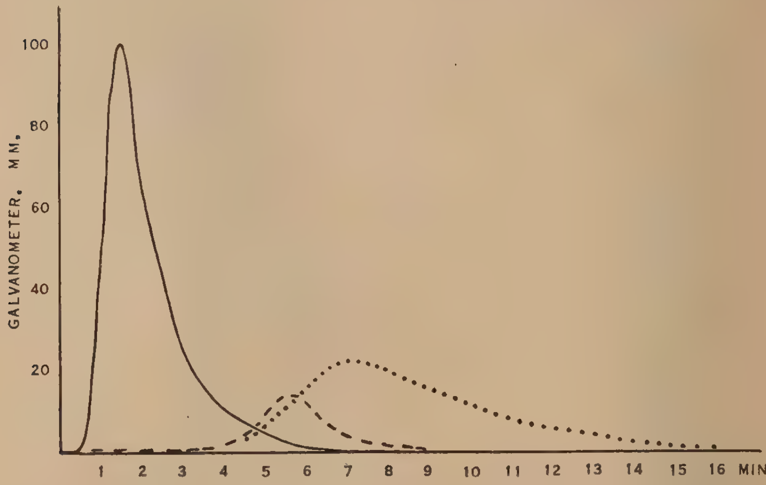

FIG. 3.—Typical record of the passage of the temperature " wave " along the larger tanks (Apparatus I) at each conditioning experiment. Continuous line=thermo-couple at A1; broken line=thermo-couple at B1; dotted line =thermo-couple at C1. Times are reckoned from the moment of putting in the switch of the heating circuit.

GENERAL PROCEDURE IN MAKING THE "CONDITIONING" EXPERIMENTS.

After being put into the tanks the fish is left to "settle down," for which a period of at least two weeks is usually needed. During this time the fish is supplied daily with food, but generally refuses it for many days, and so long as it continues to do so the food is left until the end of the day when, if still uneaten, it is removed. When the fish is taking food readily this indiscriminate feeding is stopped for a few days before starting the process of "conditioning" or association of the temperature stimulus with the subsequent giving of food. The general behaviour of fishes during the preliminary "settling down" has been already noted on p. 3. The indiscriminate feeding during this time does not involve passage upstream, the food being dropped into the deeper end of the tank near the fish. The conditioning experiments are carried out as follows :—

The observer enters the special building and locks both doors. The tanks are inspected to see that water flow, etc., is all in order. He then takes up his position (wearing rubber shoes throughout the tests) on the stool O (fig. 2) and notes the behaviour and positions etc. of the fishes during at least fifteen minutes, the temperature of the cold-water junction is read, and the galvanometer readings for each thermo-couple are taken. Then the following operations are carried out for each tank. The switch of the heating circuit (K, fig. 2) is closed to heat the water very slightly as it enters the tank. In the early stages of conditioning the heating circuit is closed for 60 sec. for the larger tanks, and 15 sec. for the smaller, these times being reduced when the minimum temperature rise which the fish can perceive is being found. Records of the galvanometer readings for each thermo-couple in the larger tanks are then noted down at 15, 30, and 60 sec. intervals, at the same time watching the fish closely. The moment the temperature at the thermo-couple closest to the fish begins to fall away from its maximum (see fig. 3 and p. 7 for typical example of changes), food is introduced into the distant food chamber by "washing" it noiselessly down the food tube with water. Pieces of mussel of a uniform size for each type of fish are used as food, one piece at each association. To the first of the two stimuli—the temperature increase—the fish shows no signs of response for a large number of tests. To the second—the food lying in the food chamber—it shows no signs of response until it is perceived (by sight, smell, etc., according to the habit of the fish). A fish such as the cod, for instance, does not react to it for several minutes (i.e. until perceived either by smell or taste or, less likely, by sight) owing to the distance of the food, but when it is perceived the fish at once starts upstream "seeking" movements, and so persists directly upstream until it gets half-way up the tank where it begins to get uncovered.

In the early stages of conditioning, it now returns to its normal position, and shortly after again goes through the same performance, repeating it several times. Its actions become progressively more excited, at each attempt going further upstream nearer to the food, and in so doing becoming more and more uncovered with water. Finally it makes a rapid splashing swim, or rather, wriggle, right into the food chamber, where it makes an attempt to seize the food, acting throughout as if in a state of great agitation. In these early stages it is usual for this to result in failure to acquire the food, whereupon the fish splashes back at great speed to its resting position without the food for which it has struggled. For several days it is not usual for the fish to go through these actions in their entirety more than once in one day, although the food is still present in the food compartment and the fish is free to fetch it. If this remains uneaten by the end of the day I remove it before leaving the laboratory. As these associations are continued day after day the fish becomes more persistent in its efforts to reach the food and less agitated by its own vigorous splashing. Eventually, when thoroughly conditioned, it takes the food without hesitation, but always, or so it appears, with great excitement, and to the end of the experiments makes the return journey with very great rapidity and "nervousness." The movements involved in getting food from the food compartment have been already described on p. 3. By continuing this regular association of temperature increase with food there comes a time when, as soon as the thermo-couple nearest to the fish shows that the temperature increase has reached that point, the fish shows an obviously "anticipatory" reaction. With fishes such as the gadoids, which maintain posture by gentle undulation of the pectoral fins, the earliest sign of conditioned response is a quickening of their undulation, followed by a rapid swim upstream, of varying extent and in its final form the whole response occurs in the way already described as the act of food-getting. It must be remembered that this now takes place before the introduction of food. In the later stages the fish, having arrived in the food chamber, continues to wait there practically "high and dry" until food is given, which it then seizes sharply and swims and splashes violently back to its normal position.

During these performances the attitude of the fish may be described as one of great excitement and its movements are rapid, alert, and vigorous; it may also show champing movement of the jaws. With sedentary fishes such as Blennius, Onos, Liparis, etc., which remain (under the conditions of these experiments) for hours or even days motionless in their tanks, the response is still more striking.

RESULTS.

It will be useful if I restate here that, having first established that the particular type of conditioned motor response could in fact be built up, the experiments were planned to find out further whether fishes would form these conditioned motor responses to the smallest temperature increment which it was practicable to apply and to measure with reasonable accuracy under the peculiar circumstances of the experiment. They were therefore first conditioned to a relatively high temperature stimulus of a strength found to be effective (an increase of from 0·4° C. to 3·0° C.). After having formed the conditioned motor response to this stronger stimulus, the temperature rise was then gradually lowered at successive trials to the lowest practicable limit of between 0·03° C. and 0·1° C. If the fishes continued to give either a complete conditioned response or some essential part of it for a further large number of trials the object of the experiment was achieved. There were a number of deaths in the preliminary and early stages of an experiment, and these are not further considered. Such deaths would very likely have occurred just as readily had the fishes been living under ordinary aquarium conditions, and were regarded as failures to become acclimatised to the changed conditions. Of the fishes which became fully acclimatised, it may be said at once that each one had given, before the completion of the individual experiment, a well-marked conditioned motor response of the type outlined in the previous section to a temperature increase of between 0·05° C. and 0·10° C., and in some instances consistently to a rise of 0·03° C. for a large number of successive trials. This is the essential result of the whole series. As the experiments were lengthy, each individual being investigated for several months, it is proposed to give a "log" of one experiment only, that on the cod, *Gadus callarias*, and to give a summary of the remainder. These histories may be divided into two series corresponding to the two types of apparatus, large and small.

A. EXPERIMENTS IN APPARATUS I.

Gadus callarias L.

The "log" of this experiment is condensed into Table I. In this record and in the brief descriptions of the other experiments a large number of subsidiary observations must of necessity be omitted, neither is it possible to give any detailed account of the temperature changes down the tank, for which the typical example quoted above (p. 8) must suffice. Throughout the paper I use such terms as "anticipatory," "sulking," "nervous," "attention," etc., in describing behaviour solely as a means to illustrate the behaviour of the fishes more graphically and in a manner which may be readily understood. The terms have merely a descriptive value.

TABLE I.

Record of Experiment on a Specimen of the Cod, *Gadus callarias* L., 20 cm. in length, showing the Process of Conditioning to a Temporary Slight Increase in the Temperature of the Surrounding Water.

size of specimen—20 cm. when started, 23 cm. when finished. Lived in the actual tank for several months before experiments were started. For full description of the actions of the fish under the various conditions see text pp. 9, 10. The times given in the "response" columns refer to the actual time subsequent to putting in the switch which starts to heat the water as it flows in. The maximum temperature rise used as stimulus from 12.v to 17.vi was 1·4° C., and was generally very close to this.

Date.	Time.	Behaviour of fish during 15 min. immediately prior to conditioning test. (Letters refer to position in tank, see Fig. 2.)	Position of fish when the observations in next two columns were noted.	Temperature increment of water in vicinity of fish at the instant of conditioned response.	Response to conditioning stimulus, e.g. temperature increment.	Response to unconditioned stimulus, e.g. food.	Notes.
12.v.3	12 00	Slow quiet swimming at C.	C	—	None during 22 min.	Fetched with very nervous actions after one preliminary attempt when it swam only half-way towards it.	Food given at B to get the fish accustomed to passing upwards.
13.v.32	14 30	do.	C	—	None during 20 min.	Fetched eagerly and at once.	do.
14.v.32	9 45	do. between B and C.	B	—	do 25 min.	do. leaving part behind.	Food given at entrance to food chamber.
17.v.	9 52	do. at C.	C	—	do. 15 min.	Fetched rapidly at once.	do.
[no further expt. between 15.v.32 and 3.vi.32 owing to personal illness.]							
4.vi.	12 10	do. at C.	C	—	do. 15 min.	do.	do.
5.vi.	11 05	do. at C.	C	—	do. 15 min.	do.	do.
6.vi.	10 20	do. between B and C.	B	—	do. 2 min.	do.	do.
8.vi.	12 30	do. at C.	C	—	do. 5 min.	Food given at 5 min. but not fetched until 18 min.	do.
9.vi.	12 35	do. at C.	C	—	do. 4 min.	do. [fetched at 15 min.]	Very active the whole time between giving of food and fetching it, dashing wildly up and down.
14.vi.	11 25	do. at C.	C	—	do. 4 min.	do. [do. 16 min.]	
15.vi.	10 15	do. at C.	C	—	do. 4 min.	do. [do. 12 min.]	
	15 05	do. at C.	C	—	do. 4 min.	do. [do. 6 min.]	
16.vi.	9 45	do. between B and C.	B	—	do. 2 min.	Food given at 3 min. fetched rapidly without hesitation.	Food now given inside food chamber, the return from which was made with great rapidity, much splashing, and signs of "nervousness."
	14 20	do. at C.	C	—	do. 4 min.	Food given at 5 min. do.	
	19 40	do. at C.	C	—	do. 4 min.	do. do.	
17.vi.	10 20	do. at C.	C	—	do. 4 min.	do. do.	
	12 50	do. between B and C.	B	—	do. 2 min.	Food given at 3 min. do.	
18.vi.	10 30	do. between B and C.	B	1·2° C.	Swimming became very rapid, excited dashing up and down.	do. 3 min. do.	
	12 30	do. do.	B	0·6° C.	Same excited actions as at 10 30.	do. do.	
20.vi.	16 30	do. do.	B	0·3° C.	Very excited swimming up and down, going almost to food chamber several times.	Food given at 5 min. Excited actions continued, food taken with great nervousness at 14 min.	
21.vi.	12 20	do. do.	B	0·3° C.	do.	do. fetched at 18 min.	
	17 20	do. do.	B	0·3° C.	do.	do. 12 min.	
22.vi.	11 45	do. do.	B	0·2° C.	do.	do. 8 min.	
	12 50	do. do.	B	0·4° C.	do.	do. 8 min.	
	16 10	do. do.	B	0·7° C.	do.	do. 14 min.	
23–24.vi.	No expt.						
25.vi.	20 35	do. do.	B	0·23° C.	do.	do. 8 min.	
	21 20	do. do.	B	0·37° C.	do.	do. 8 min.	
26.vi.	11 05	do. do.	B	0·17° C.	do.	do. fetched immediately.	
	12 10	do. do.	B	0·25° C.	do.	do. fetched at 10 min.	
	15 20	do. do.	B	0·13° C.	do.	do. do. once.	
27.vi.	9 50	do. do.	B	0·10° C.	do.	Food given at 3·5 min. Fetched at once.	
	11 40	do. do.	B	0·15° C.	do.	do. do. 15 min.	
	12 50	do. do.	B	0·23° C.	do.	do. do. 15 min.	
	15 45	do. do.	B	0·23° C.	do.	do. do. 15 min.	Some adjustments made in apparatus after last test on 27th.

28.vi.	12 10	Fish "sulking" in deepest corner of tank at C.	C	[1·12° C. (max.)]	No reaction whatever in 11 min.	Food given at 11 min. Not taken and no signs of interest taken in it. Removed at 13 05.	
	17 20	do.	C	[1·35° C. (max.)]	do.	do. Removed food at 18 30.	
29.vi.	No expts.	Deepened water slightly to facilitate passage completely into food chamber.					
30.vi	do.	Fish still "sulking" as on 28th.					
1.vii.	15 40	do. up till midday, then swimming as usual between B and C.	B	0·90° C.	Very excited swimming response as before the 27th.	Food given at 4 min. but not taken by 17 00 so removed.	
2.vii.	No expt.	Fish "sulking" and not looking well.					
3.vii.	do.	Fish apparently normal again in appearance and behaviour.					
4.vii.	6 50	Fish now swims more frequently at about centre of tank, near B.	B	0·08° C.	Very excited, went directly to food chamber, stayed there till food was given 10 sec. later.	Food taken at once.	
	12 05	do. almost stationary	B	0·08° C.	Exact repetition of last.	do.	
	16 50	do. do.	B	0·05° C.	do.	do.	
5.vii.	9 15	do. do.	B	1·00° C.	do.	do.	
	12 00	do. do.	B	1·00° C.	do.	do.	
	19 50	do. do.	B	1·00° C.	do.	do.	
6.vii.	11 45	Moving slowly about near T.C. 2 (B).	B	0·05° C.	Went immediately to food chamber.	do.	
	15 10	do.	B	0·05° C.	do.	do.	
7.vii.	9 50	Keeping more or less still with dorsal part of body out of water, about 1 foot above B.	See last col.	0·05° C.	do.	Food delayed for 5 min., during the whole of this time the fish stayed on its side in the food chamber, wriggling and nosing about for food. Response now very powerful.	
	12 10	do.	do.	0·08° C.	do.	do. [same delay].	
	19 45	do.	do.	0·05° C.	do.	do. [do.]	
8.vii.	15 45	do.	do.	0·05° C.	do	Food given immediately on entering food chamber.	

[Owing to the habit this fish now had of keeping well up the tank the level of the water was now reduced to its previous height (i.e. as before 28.vi).]

9.vii.	10 05	Swimming slowly between B and C as before, but occasionally passing B.	B	0·05° C.	Repeated rapid and excited dashes to mouth of food chamber, but no actual entry.	Food given 2 min. after first rapid swim to entrance but it was not actually fetched for a further 2·5 min. The lower water level necessitates much more splashing in reaching the chamber.	
10.vii.	No expt.						
11.vii.	10 05	Swimming rapidly up and down [possibly due to hunger, as no food yesterday].	B	0·05° C.	Extremely violent dash straight into food chamber.	Food given immediately on entering food chamber, snapped up at once.	
	11 05	Swimming slowly between B and C.	B	0·05° C.	Exactly as on 9.vii.	do.	
12.vii.	10 50	do.	B	0·05° C.	Immediate swim directly into food chamber.	Food given at once and taken quickly. The fish continued to make repeated swims into the food chamber during the next 20 min., until an even temperature again supervened.	
	16 05	do.	B	0·08° C	do.	do.	do.
13.vii.	11 00	do	B	0·10° C.	do.	Food given and taken at once. Then rested quietly between B and C.	
	15 10	do.	B	0·05° C.	do.	do.	do.
14.vii.	10 35	do.	B	0·05° C.	do.	do.	do.

[15.vii. No expt. Demonstrations to Mr. Storrow caused a certain amount of disturbance.]

16.vii.	9 25	Kept almost still by T.C. 2 (B).	B	0·05° C.	Dashed wildly up into food chamber, and then back to very opposite end of tank with extreme rapidity. It then continued to make repeated dashes from C to B, but there stopped suddenly short, as though violently inhibited.	Food taken with nervousness only after 15 min.	This very remarkable response is clearly connected with the demonstrations of yesterday.
17.vii.	10 00	Watched during 30 min. fish swimming slowly around at B, occasionally making short rapid swims (as if in anticipation) between B and the food chamber. It sometimes stayed there for nearly a minute showing evidence of keen attention.	B	0·16° C.	Almost exactly as yesterday, continuing even longer, for 30 min.	Food taken at 30 min.	do.

[17.vii. At noon raised the level of the water back to the level of between 28.vi. and 8.vii. The fish now took up its old position well above T.C. 2, between the mid-length of the tank and the food chamber, showing continuously signs of keen attention.]

18.vii.	No expt.						
19.vii.	9 20	Swimming slowly between B and C, sometimes motionless for several minutes just above B.	B	0·05° C.	Immediate swim into food chamber, where it stayed waving its tail and nosing about until food was given.		
	15 30	do.	B	0·22° C.	do.	do.	do.
20.vii.		Fish removed to aquarium tanks prior to my going on leave. While I was away it jumped out of its tank and died on Aug. 8th, 1932.					

Among the more interesting points in the experiment with this fish are the following. The earliest signs of conditioning appeared at the 18th association of temperature with food (18.vi). This was followed by a period when the conditioned response was incomplete—lasting until the 37th association (1.vii). The first complete conditioned response occurred at the 38th association (4.vii). It may be readily seen that a temperature of 0·05° C. was sufficient to produce the conditioned response throughout the greater part of the experiment, which was brought to a premature conclusion on 19th July, 1932.

Gadus merlangus L.

Individual whiting were found to be difficult to acclimatise to these conditions. This experiment was therefore begun with a group of three young specimens, each of a length of 12 cm., which together settled down readily, after being placed in the apparatus on April 30th, 1932. Like the cod just described they normally swam slowly up and down at the deeper end of the tank, and there was also, as with that fish, considerable hesitation over the performing of the final part of the act involved in getting food until the experiment was well advanced. One fish (which could be easily recognised as having a darker mouth than the others) was generally the first to respond both to the temperature and to the food stimulus, as well as being the first to show any signs of conditioning. The first conditioning experiment was made on May 13th. On June 14th (at trial 10) the three fishes were swimming slowly about when the "leader" (for so we may conveniently call the dark-nosed individual) happened to arrive at the middle thermo-couple at the same time as the warmed water which was passing slowly down. It at once rapidly increased its rate of swimming and went without hesitation straight on and into the food chamber, but not waiting, however, for the food which was shortly to follow. It fetched this very nervously after a few minutes. The other two fishes showed no conditioned reactions, nor did they fetch the food for some considerable time. For the next three days this was a typical picture of events at each association. On June 18th all three, beginning still with the leader, showed conditioned responses before food was given. At the 25th trial (June 25th), the leader and one other gave a complete response, together swimming with extreme rapidity direct to the food chamber, the third following shortly afterwards. The next day all three gave a complete conditioned response at the same instant. From the earliest signs of conditioning all three showed evidence of extreme nervousness when carrying out the responses. On June 27th one of them was found to be very inflated and died during the night after removal to one of the aquarium tanks. Another died on July 2nd, leaving the experiment to be concluded with the "leader." By the 42nd trial this fish was giving complete conditioned responses to temperatures of 0·05° C. During the course of the experiment various adjustments of depth of water were made from time to time with results similar to those with the cod. I was absent on vacation between July 20th and August 16th. For this period the fish was removed to one of the aquarium tanks where it was fed with others in the usual routine manner. On returning it to the experimental apparatus in the special building it refused food and " sulked " until August 23rd. The following day this came to a sudden end when the fish gave a complete conditioned response, going directly to the food chamber in response to the temperature increment. This showed complete retention of the conditioned response after thirty days' absence from the apparatus. Between August 25th and Sept 6th temperature increases of 0·03°–0·07° C. consistently gave perfect conditioned responses, and again on Sept. 12th., after I had been away from the laboratory since Sept. 7th, during which time the fish was left in the apparatus without food and entirely free from disturbance. It was now necessary to go more fully into the question as to whether the temperatures given above (and indeed throughout the whole series) were those of the actual point of stimulation. This cannot be satisfactorily answered until more is known about the distribution of the end-organs for temperature perception. But the problem was narrowed down by placing thermo-couples at very short intervals between the surface and bottom, for it has already been mentioned that relatively warm water travels down the surface layer very much more rapidly than in the lower layers. It was definitely established that the response began only when the thermo-couple which was placed at a depth corresponding to the upper part of the body of the fish (excluding the dorsal fin) gave the readings from which the temperature increments were calculated. The experiment was concluded on Sept. 24th, 1932. Since Sept. 12th temperature increments of 0·03°–0·13° C. (with one occasion when no response was shown until a rise of 0·33° C. was indicated) had been adequate stimuli. Total number of associations 73.

Gadus virens L. Size 14 cm.

Started October 6th, 1933, and settled down readily. Two individuals of this species previously tried had refused to settle down. The first conditioning experiment was made on October 11th. Its general behaviour was closely similar to that of the other gadoids already described. The first sign of conditioned responses to temperature increments was shown on October 26th (24th association). These actions, both in their early and in their completed states, closely resembled those of the cod and whiting, i.e. in the early stages—short, rapid, to and fro swimming, passing once or more to the upper parts of the tank, but not actually entering the food-chamber, the whole action being carried out with signs of considerable "nervousness." This incomplete response was given until November 9th. On this date (49th association) the complete conditioned response including entry to food chamber was made, but with great rapidity and nervousness, this type of reaction occurring until November 29th (71st association). Then followed a period lasting until December 5th, when the response was carried out completely but with less evident signs of nervousness, to be followed by the last period lasting until December 15th, during which the highly nervous type of response reappeared and persisted. The total number of associations was 83, of which at numbers 61 to 83 the adequate temperature stimulus was an increment of between 0·06° and 0·10° C.

Raniceps raninus (L.). 17 cm.

This is one of our rarer fishes and is not easy to keep in captivity. The specimen used was caught on a fisherman's line in November, 1931, and kept under aquarium conditions before being transferred to the experimental building on November 11th, 1932. During these twelve months it appeared to be in exceptionally fine condition, but after its transference it refused food for many weeks and was not feeding readily enough for experimental purposes until January, 1933, the first association of temperature and food being given on January 9th. Its normal resting behaviour was characteristic—"lurking" at the lowest corner of the tank (C), occasionally passing almost imperceptibly a short distance up the tank with slow waves of the tail, then backing again with the same smooth action. When disturbed it could be both vicious and vigorous in its actions. Temperature increments of approximately 0·4° C. were used in the early stages of conditioning.

No change in the normal resting behaviour was shown to any of these increments until the 31st (on February 2nd). At this trial the fish started to swim slowly upstream in response to the temperature stimulus and went straight on to take the food from the food chamber when it was given 30 sec. later. No further complete responses were given for several weeks—although the fish continued without exception to carry out the first parts of the reaction immediately following the temperature stimulus. From February 13th to March 14th food was entirely refused, but weak anticipatory responses continued to be shown to the temperature rise. On March 14th (trial 56) weak anticipatory responses were followed by actual consumption of the food—fetched from the food chamber. The 61st trial (March 21st) produced a complete conditioned response, the fish splashing rapidly upstream on reception of the thermal stimulus. With occasional modifications and periods during which no food was taken the fully formed conditioned response was given to most of the trials with the thermal stimulus from this date to the conclusion of the experiment on June 8th after 147 associations. The magnitude of the stimulus was lowered gradually between March 21st and April 18th, until by the latter date conditioned responses were given to increments between 0·05° C. and 0·10° C., and continued to be given to these small increases up to the end of the experiment.

Pleuronectes platessa L.

This species readily settles down to the experimental conditions. An experiment with a ♂, 17 cm. long, was started on August 24th, 1932. Its normal resting behaviour was generally to stay motionless in one position for long intervals of time mostly at about the centre of the tank, touching the central thermo-couple. The first conditioning experiment was made on August 26th, the fish showing no reaction whatever to the temperature increment (1·0° C.), but fetching the food readily from the food chamber in its slow, hesitant manner. Owing to the restricted size of the entrance to the food chamber the fish had difficulty in getting out of it again, and eventually backed out, a course which it was always compelled to adopt. The earliest evidence suggesting that the association between temperature and food was being formed was seen so early as the 11th association (September 6th), when, after making such anticipatory actions as eye-movements directed towards the food chamber, and characteristic forward jerks, the fish passed into the food chamber after ten minutes. The food was withheld until the responses ended at their goal. At the next two trials on the same day slight forward movements were the only response to the thermal stimulus. During the following three days no experiments were made, but a complete conditioned response of the slow, jerky nature typically given by this species was given at each of three separate trials on September 12th. Between September 13th and 15th (i.e. from trials 19 to 23) the temperature increase was lowered at each successive trial; from September 16th onwards it was kept at 0·1° C. or lower (minimum actually producing response 0·06° C.).

The experiment was finished on October 25th after 71 associations, temperature increments below 0·1° C. acting as stimuli from trials 24 to 71. The stationary habit of this fish permitted the measurement of the temperature increment at the moment of response to be made with a much greater degree of accuracy than with the fishes previously described.

A smaller specimen (8·5 cm.) of the same species was investigated in Apparatus II, between October 6th and December 15th, 1933, during which it was given 78 associations of temperature and food. The first conditioned responses appeared at trial 21, the complete response at the 27th, whilst temperatures below 0·1° C. (minimum 0·05° C.) were effective conditioning stimuli from the 35th association (November 18th) to the conclusion.

Cottus scorpius L. 22 cm., ♂.

Cottus scorpius and *C. bubalis* are fishes which are well-suited to this type of experiment, being ready feeders, easy to keep in good health, spending long periods motionless in one position, and such movements as they do make are sharp and decisive in character.

This specimen was placed in the apparatus on June 26th, 1933 and the first conditioning experiment made on June 28th. No signs of awareness of temperature increment were shown until the 12th association with food (July 4th). Shortly after the maximum increase of 0·6° C. had been reached the fish made a short jerky movement forward—rested a few seconds—then another movement—and so on until it reached the middle of the tank, at which moment food was given in the food-chamber.

It then completed the response and dashed wildly back to its normal position at the deeper end. The complete conditioned response was given so early as trial 16 (July 5th). By trial 20 (July 6th) the temperature stimulus was reduced to 0·2° C. and at trial 23 to 0·1° C. Until the conclusion of the experiment after 88 associations (September 7th) the effective stimulus remained between 0·05° C. and 0·1° C. Some modification of behaviour took place during the course of the experiment, the fish coming to adopt the habit of staying at a point midway in the tank in spite of the fact that under these conditions its head was well out of water. The conditioned responses given in the later stages were carried out with actions so rapid, and splashing so violent as to make it very difficult to observe both the galvanometer scale and the fish at the instant of reaction.

B. Experiments in Apparatus II.

Pleuronectes flesus L. 15 cm. long.

Experiment started on August 10th, 1933. This fish was stationary for long periods close to the outflow, and generally had the thermo-couple junction in direct contact with it. The first conditioning experiment was made on August 17th. No responses were shown to the temperature increment until the 20th association (September 1st), when the fish moved slowly round and looked "expectantly" towards the food chamber; it made no further move until food was given two minutes later. The next day it went rapidly to the food chamber when the temperature increase was 0·6° C. and remained there until food was given. No tests were made on September 3rd, whilst a negative result was given on September 4th. I was away from the laboratory for the following seven days during which time the fish was removed from the special building to an aquarium tank, being replaced in the apparatus on

September 13th. At two trials on September 14th, being the 24th and 25th since the beginning, no conditioned response was seen, but at the 26th and 27th (September 15th) the complete swim to the food chamber was made before food was given. The conditioned response then remained stable until the conclusion of the experiment at the 59th association (October 5th), for the last 20 of which no increment greater than 0·1° C. had been used as the conditioning stimulus, the minimum being 0·05° C. The experiment was ended mainly because the fish had become too long to turn round comfortably.

Pleuronectes platessa L. Length 8·5 cm.

Summarised above on p. 17.

Spinachia vulgaris Flem. Length 12 cm.

Put in apparatus on October 6th, 1933. For some time swam restlessly up and down, frequently getting entirely out of water at the food chamber, but settled down after a few hours. A small plant of Fucus was found useful in the deeper end of the tank, as the fish took cover among its fronds, and stayed amongst it throughout the experiment. Conditioning experiments were started on October 11th, the fish proving to be an easy subject as it fed readily and viciously. No response was given to the temperature increment until after 41 associations with food (November 5th). At the 41st temperature stimulus the fish turned awkwardly round (its normal position being head downstream at the deep end, concealed among the Fucus) and went directly to the food chamber where it was given food on its arrival. No further conditioned behaviour was seen until November 11th at association No. 53 when the fully formed response was again given. Such sudden changes in conditioned behaviour are unusual unless for some clear reason such as obvious loss of appetite. The temperature increment was lowered between November 11th and 25th until it was down to the range 0·05° C.–0·10° C. which was then used as stimulus and found effective up to the end of the experiment on December 15th after 84 associations.

Gobius (Gobiusculus) flavescens Fab.

(*Gobius ruthensparri* Euphrasén.) ♂, length 6 cm.

Put in apparatus on October 6th, 1933, and settled down at once, showing no signs of uneasiness whatever, and taking food readily the same day. Owing to its small size the depth of water for this species was reduced to 2·5 cm. at the deeper end and shallowing to nothing in the food chamber. Neither this species nor Spinachia showed any discomfort whilst wriggling along out of water and wriggled backwards readily with no undue haste after taking the food. The normal resting behaviour consisted of alternate rests and sallies, and it was frequently observed chasing bubbles or any small particles that might happen to fall on the surface of the water. Conditioning started on October 11th, the full conditioned motor response being given so early as October 18th after 14 associations. The temperature increment acting as conditioning stimulus was lowered to 0·1° C. by October 28th (after 26 associations) and was maintained between 0·05° C. and 0·1° C. from then until the conclusion on December 15th after 77 associations. Of these further 51 trials, 15 produced no response (December 6th to 12th) but food was also refused on those days. Only rarely did this fish show any of the very rapid nervous responses of the gadoids, generally going straight upstream into the food chamber with a series of rapid darts, the final six inches, which necessitated wriggling, excepted.

Crenilabrus melops (L.).

A young specimen, 6·5 cm. long, taken from a rock-pool at Cullercoats on October 4th, 1933, and put in the experimental apparatus on October 6th. Its normal behaviour was to rest in contact with one of the lower corners of the tank, but making occasional swims round the sides of the tank. Conditioning began on October 11th. Owing to the relatively greater depth of body, it was found that this species could not negotiate the final six inches of the passage to the food chamber unless there was sufficient water present to enable it to get along in at least a semi-vertical position. Probably for this reason it could not be conditioned to make the full swim, always stopping short when the dorsal part of the body was clear of the water. Anticipatory actions were seen after 29 associations (October 31st); these were champing of the jaws, upturning of the eyes to the food tube and waving of the pectoral fins. No further evidence of conditioning was seen until trial 39 (November 8th) when the anticipatory actions again appeared, whilst even partial swimming to the food chamber did not occur until trial 46 (November 15th) and the full swim (modified as above) not until trial 53 (November 21st). Temperature increments between 0·05° and 0·10° C. were then used successfully until the conclusion of the experiment on December 15th (total number of associations—71).

Liparis montagui (Don.). Length 9 cm.

This is a small and inconspicuous littoral fish with the ventral fins united to form an adhesive disc. In the apparatus the fish stayed motionless for many hours at a stretch, adhering to the bottom or sides of the tank, generally close to the outflow. Small pieces of shore-crab liver were used in place of mussel as food for this and the next species. The fish was put in the apparatus on October 6th, 1933 and the first conditioning experiment made on October 11th, but for a few days food was not as a rule eaten until many minutes had passed. Anticipatory reactions, consisting of curling and uncurling the tail (the body staying adherent and motionless), were given at the 26th association of temperature increase and food (October 28th). These continued to be given without any further motor response until the 36th association (November 6th) at which test, on perceiving the thermal stimulus the fish turned round and went upstream searching and "nosing about" with rapid circular movements as it went to the food chamber. This remained the general picture of the full motor response until the end of the experiment on December 15th after 71 associations. Only temperature increases between 0·03° C. and 0·10° C. were used after November 6th.

Cyclopterus lumpus L.

The specimen used was a very young one, only 3 cm. long, of a fish belonging to the same family as the last and characterised likewise by the union of the ventral fins to form a circular adhesive disc. Its general behaviour was closely similar to that of Liparis, and the experiment progressed in much the same way, the fish being put in the apparatus and receiving the first conditioned stimulus on the same dates. No anticipatory reactions were seen in this fish but this may have been due to the difficulty of observing such reactions in so small a fish with the low magnification of the periscope. It gave a full conditioned response of swim to and entry into the food chamber on November 4th (after 32 associations). Food was usually taken readily and quickly but was not infrequently ejected and reswallowed several times before the fish finally left the food chamber and returned to its usual position. Temperature increases of 0·05–0·10° C. only were used between November 5th and the conclusion on December 15th (after a total of 67 associations), the conditioned response remaining quite stable. It is interesting to find that so young an individual forms the conditioned response as readily as mature fishes.

Zoarces viviparus L.

Put in the apparatus on March 10th, 1934, but did not feed until March 17th, and the first conditioning experiment was made on April 3rd. Its general behaviour was well suited to the purpose as it remained motionless, curled up in one corner, for long intervals. The temperature stimulus evoked anticipatory reactions on April 14th after 25 associations with food, and the full conditioned response was given at the 26th at which test the increase in temperature used was 2° C. On April 18th the fish swam rapidly and excitedly to the food chamber in response to a rise of

0·03° C., and a stimulus of between 0·03° C. and 0·05° C. was used for the remainder of the experiment until May 28th (associations 31 to 95).

Blennius pholis L.

A specimen 15 cm. long was put in the apparatus on March 10th, 1934. The first association of temperature increase with food was made on April 3rd. No response was given to the thermal stimulus until the 33rd association with food (April 19th), when the temperature alone produced the anticipatory conditioned response typical of this species. A complete response following anticipatory movements was given at the 37th, the anticipatory responses occurring to a rise of 0·03° C., the full response to a rise of 1·0° C. The temperature increase at each association was then successively lowered ; between associations 49 and 95 (the last), lasting from April 30th to May 28th, the stimulus was restricted to a rise of 0·03°–0·05° C., full conditioned responses being readily given since trial 37.

Onos mustela (L.).

A specimen 14 cm. long was put in the apparatus on the same date as the two last, and experiments began also on April 3rd, 1934. In normal behaviour it is somewhat similar, except in its response to food, the acquisition of which is determined by olfaction and gustation instead of by vision. When food was put in the food chamber the fish gave no sign of movement for a minute or so ; it then started random circling movements, going steadily nearer to the food, and frequently passing close to it without apparently noticing it until some part of its body actually came into contact with it, when it would turn round sharply and sieze it. The conditioned response was dominated by these same features. After 12 associations of temperature increase with food (April 7th) these seeking movements were initiated by the temperature stimulus alone, continuing until food was acquired.

At the 15th trial it progressed in this way upstream in response to a temperature increase of 0·03° C. and remained in the food chamber "excitedly" floundering about until food was given. It continued so to respond to the same small increment until an accident caused its death after 29 associations on April 17th.

Centronotus gunnellus (L.), 19 cm. in length.

The general course of this experiment was not unlike that on Zoarces, both the normal and the conditioned behaviour of the two species being similar. It was put in the apparatus on March 10th, 1934, given its first association of temperature with food on April 3rd, and gave the full conditioned response on April 24th after 39 associations, continuing so to do until the conclusion on May 28th. From associations 47 to 95 (April 28th to May 28th) only temperature increments of 0·03–0·05° C. were used as conditioning stimuli. The fish showed no anticipatory reactions other than orientation of the whole body or an occasional tail movement which passed directly into the carrying out of the whole response.

Chirolophus galerita (L.) [=*ascanii* (Walbaum)].

A specimen 19 cm. long of this uncommon species was conditioned to a temperature increase as far as the early stages, but died accidentally before any attempt had been made to ascertain the minimum rise to which it would respond. Twenty-five associations were required for the production of the conditioned response, the behaviour of the fish throughout being very similar to Centronotus.

Nerophis lumbriciformis (Pennant).

This is a very difficult species to work with on these lines, feeding being erratic; only very small pieces of crab's liver were taken, and those but occasionally, although the fish appeared thoroughly healthy and is still alive (Dec. 1935) after more than three years' experiments with one stimulus or another. The specimen (22 cm. long) was placed in the experimental tank on March 10th, 1934 and received its first association of temperature with food on April 3rd. A small piece of the brown seaweed, *Halidrys siliquosus*, was provided as a natural means of the protective concealment characteristic of the pipe-fishes. Its normal resting behaviour was to remain with the greater part of its body concealed amongst this alga. The fish was not seen to be affected by any of the sudden increases in temperature (none exceeding 2·0° C.) until May 16th, 1934 (association 56), when the fish slowly uncurled its tail and then swam rapidly upstream to the food chamber. During a large number of these 56 associations the food was not taken nor was any apparent interest displayed when it was given. There can be little doubt that the long time (six weeks) taken to condition this fish is due to the difficulty of feeding. It was remarkable that the full response was given consistently to all the remaining trials, although these were few, as the experiment was finished on May 28th at the 76th association. From May 18th (association 59) temperatures of 0·07° to 0·10° C. were used as conditioning stimuli with no apparent reduction in the strength or constancy of the conditioned response.

Cottus bubalis Euphrasén.

The results with the larger specimen of the allied species, *Cottus scorpius*, were repeated with a smaller specimen of this species (8 cm. long), the experiment being started on March 10th, 1934. Twenty-seven associations were required for the production of the complete conditioned response. One hundred and eight associations in all were given between April 3rd and May 28th. The general nature of the conditioned response was similar to that of the larger species. For the last 54 trials (April 26th to May 28th) the effective stimulus was in no instance higher than 0·05° C. and was for the most part kept at 0·03° C.

General Summary of Results.

The main features of the individual experiments in both series may be conveniently summarised in the following table (Table 3).

TABLE 3.

Summary of Experimental Results.

Species.	Duration of expt.	Number of associations required for production of conditioned response to thermal increase.	Total number of associations in experiment.	Minimum effective thermal conditioned stimulus. ° C.
Spinachia vulgaris Flem.	6.x.33–15.xii.33	41	84	0·05
Nerophis lumbriciformis (Pennant)	10.iii.34–28.v.34	56	76	0·07
Gadus callarias L.	12.v.32–19.vii.32	18	61	0·05
Gadus merlangus L.	30.v.32–24.ix.32	10	73	0·03
Gadus virens L.	6.x.33–15.xii.33	24	83	0·06
Onos mustela (L.)	10.iii.34–17.iv.34	12	29	0·03
Raniceps raninus (L.)	11.xi.32–8.vi.33	31	147	0·05
Blennius pholis L.	10.iii.34–28.v.34	33	95	0·03
Chirolophis galerita (L.)	18.iv.34–9.v.34	25	33	—
Centronotus gunnellus (L.)	10.iii.34–28.v.34	39	95	0·03
Zoarces viviparus (L.)	10.iii.34–28.v.34	25	95	0·03
Gobius flavescens Fab.	6.x.33–15.xii.33	14	77	0·05
Pleuronectes flesus L.	10.viii.33–5.x.33	20	59	0·05
Pleuronectes platessa L.	24.viii.32–25.x.32	11	71	0·06
	6.x.33–15.xii.33	21	78	0·05
Cottus scorpius L.	26.vi.33–7.ix.33	12	88	0·05
Cottus bubalis Euphrasén	10.iii.34–28.v.34	27	108	0·03
Cyclopterus lumpus L.	6.x.33–15.xii.33	32	67	0·05
Liparis montagui (Don.)	6.x.33–15.xii.33	26	71	0·03
Crenilabrus melops (L.)	6.x.33–15.xii.33	29	71	0·05

Discussion and Conclusions.

More stress is now being laid upon the economic aspects of "fundamental" research than was done when these studies were begun. It is proposed therefore to briefly discuss here the bearing of these experimental results upon fishery research.

The present state of knowledge upon temperature and its relation to fishes can be put under three heads :

1. The direct effect of abnormally high or low temperatures.
2. Experimental demonstrations of temperature perception.
3. Observations made in the course of routine fishery research work at

sea or in the field from which it has been concluded that temperature affects movements or migrations of fishes.

To the standpoint of the present paper only the last two are relevant.

The published experimental work upon temperature perception *per se* is slight, and is limited to work carried out with the gradient tank of Shelford and Allee (**7**). Wells (**15**), working with fresh water fishes, concluded that they detected and reacted to variations in temperature of 1° C. (·1° C.?*) and found all the species equally sensitive. Shelford and Powers (**8**), using marine fishes, obtained " good reactions with a difference of 0·6° C. in the length of the tank. Fair reactions were obtained with a difference of 0·5° C. and since the fishes often turned round near the centre it appears that they recognised a difference of 0·2° C." These " preference " experiments must be regarded with caution. The mere fact of a fish turning round in the centre of a tank, at a point moreover where water is overflowing, is not a sufficient basis for the statement that they react to 0·2° C. or, as in Wells' experiments of 1° (·1° C.).*

Miles (**5**), using the same method, concluded : ". . . I made a slight investigation of the sensitivity of blennies to temperature changes using Shelford and Power's gradient tank, differing by 3° C. in a length of 35 cm." He says " it seemed unwise to use much of the limited time upon these experiments." . . . yet " it is probably true that blennies are not readily sensitive to small differences in temperature."

Under the third heading, *speculation* upon the effect of temperature on fish movement is frequent. It is not necessary to consider these papers in detail, and for a summary of them see Chidester (**3** ; pp. 87–89) ; many of them may be summarised in the remark " . . . under stress of circumstances, extreme heat or cold, fish *seek* deeper water " (Lumby and Atkinson, **4**). Direct observations of conditions in which fish are said to have responded towards situations through the action of temperature are few. Ward (**14**) says that salmon when ascending rivers to spawn, upon encountering streams with a difference of 1° F. or more *select* the stream with the lower temperature. The most lengthy, as well as the most recent, observations of this class are those of Thompson (together with those of Sleggs **9**) upon the relation of cod catches to water temperature in waters operated from Newfoundland. In his earlier papers on this subject Thompson (**10**, **11**, **12**) gives no downright statement as to the precise nature of the relationship (other than that of a positive statistical correlation) which the temperature bears to the fish. But he qualifies certain anomalies by saying (**11** ; p. 76) of certain shallow waters that they were such as " cod might be *wary*† of occupying owing to the liability of sudden temperature changes." Here he directly implies, as we would ordinarily put it, conscious selection of environment. Therefore, when he says (**11**; p. 76): "These results seem to be decisive and to indicate that for Grand Bank a sharp line of division can be drawn (in spring) between waters of just below and waters of just above zero temperature. Below zero cod are scarce, while at a mere half-degree above zero they can be plentiful" it would seem that, whilst it might just as well have been that the fish were found under these conditions merely through the "set" of hydrographical factors, Thompson considered that they were there because they chose to be there. That this is the interpretation he would give of the relationship is finally made clear in his last paper where he says (**13**, p. 25): "The 1934 results *clearly indicate the conscious quest for low temperatures*,* since the skipper found that at these only did they secure large cod." None of the psychological expressions italicised in these quotations are logical deductions from the observed facts. Before the facts may be even interpreted in this way it is essential to show that behaviour of a type which may be looked upon *ordinarily* in this manner is exhibited by fishes to such temperature conditions. In other words, it must be clearly established that small differences in temperature have, as E. S. Russell puts it, *valency* (Russell, **6**) for a fish.

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* It is not clear which of these figures is the correct one. He says 1° C. in one place, ·1° C. in two places ; one of these must be a misprint.

† The italics are mine.

These experiments have made it clear that in the discriminatory perception of temperature a fish is provided with a sensory field which is so acutely sensitive as to be of obvious value in directive movements. They establish in fact the first premise needed for the proof of such deductions as that fish make a "conscious quest for low temperatures" (Thompson, *vide supra*) and other speculative assertions of a like nature.

Those points of essential value to the primary object of this series of studies will be discussed at a later date.

I wish to thank Prof. A. D. Hobson, M.A., and Dr. E. J. Allen, F.R.S., for their valued criticisms of the manuscript.

SUMMARY.

By the use of a "conditioned response" technique it has been shown that teleostean fishes respond "purposively" to an increase in temperature of the water surrounding them of between 0·03° C. and 0·10° C. It is probable that the former figure is true for all the species investigated, but it has only been practicable to establish it with certainty in a few sedentary forms.

The bearing of the results on fishery problems is discussed.

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* The italics are mine.

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The Size of Diatoms.

I. The diameter variation of *Rhizosolenia styliformis* Brightw. and *R. alata* Brightw. in particular and of pelagic marine diatoms in general.

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With one Plate and 12 Figures in the Text.

THE investigations of which this paper is a first contribution owe their inception partly to the need of establishing the identity of great patches of the diatom *Rhizosolenia styliformis*, which from time to time interfere with the East Anglian Herring Fishery, and partly to a desire to find out whether there occurs among diatoms the tendency, which appears to be broadly true in the zooplankton, for individual organisms to be larger in colder areas and at colder seasons.

For this purpose the present paper takes the form of a study of diameters. By this means it has been possible to trace the origin of the *Rhizosolenia styliformis* patch arising in the south-west swirl area of the Dogger Bank in 1934 and to establish its independence of another patch system off the Firth of Forth. The consideration of diatom cell diameters in relation to the temperature of the habitat has revealed, so far as it has been pursued, a result that was surprising and quite unexpected. Cell diameters in diatoms, instead of increasing with a lower temperature in the way that zooplankton size tends to do, appear to decrease.

I am indebted to Dr. W. R. G. Atkins and Mr. G. M. Spooner of the Marine Laboratory, Plymouth and to Dr. John Hart of the "Discovery" Expedition for reading the MS. of this paper and for the helpful criticisms and suggestions they made as a result of this.

RHIZOSOLENIA STYLIFORMIS.

In 1932 and 1933 the diatom *Rhizosolenia styliformis* was particularly abundant in the North Sea and during that time, and also in 1934, the origin and movements of the dense patches in which this species is wont to occur have been subject to extensive investigations which are published elsewhere (Savage and Hardy [**16**] and Savage and Wimpenny [**17**]). Here it is sufficient to say that Rhizosolenia appears to be a regular inhabitant of the S.W. Dogger Bank Swirl. It is also present in the Firth of Forth Swirl and there is no doubt that these areas may be seeded from the north by the Atlantic water of which it is an inhabitant. There is no evidence of the species having been observed to enter the North Sea through the straits of Dover.

The observational data in this paper consists of diameter measurements for samples usually of 100 individuals taken, mainly by the Hensen net, from positions in important patches during the course of the investigation just mentioned. These positions are given in Table I. The measurements (Table II) were made with the aid of a micrometer in a No. 10 eye-piece and using a 4 mm. objective. The arbitrary units thus obtained are approximately equal to 4μ. Care was taken to make the sampling free from bias by spreading a mixed sub-sample on the surface of a ruled slide. Usually

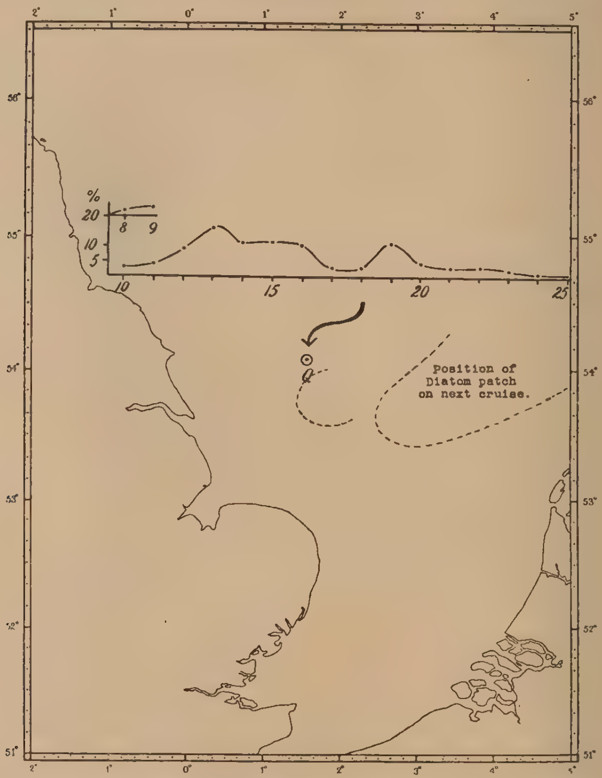

FIG. 1.—The percentage of *Rhizosolenia styliformis* cells at different diameters from station Q, cruise H, October, 1932. The units of the abscissa are approximately equal to 4μ. The position of a dense patch of this diatom is shown by dotted contours.

all whole cells cutting a ruled line were measured in succession until the desired number was obtained. In sparse samples both whole and broken cells were measured in this way, and occasionally every available cell, whole or broken, in one or more sub-samples had to be dealt with. The results of these measurements showed multimodal populations recalling those revealed in Wesenberg-Lund's classical work on the fresh-water diatoms of Denmark (**19**). The observations may now be dealt with year by year.

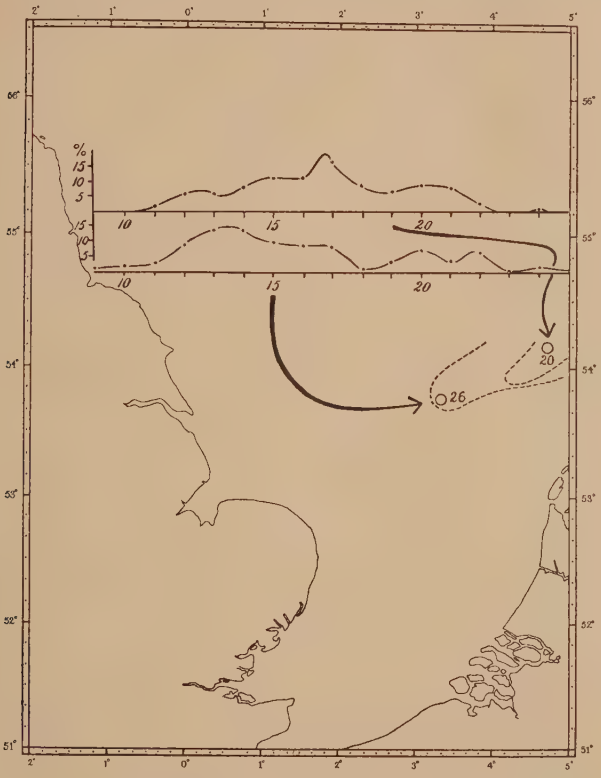

Fig. 2.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 20 and 26 of cruise J, October 1932. The position of a dense patch of this diatom is shown by dotted contours.

1932.

In October of this year successive cruises revealed a patch moving round the southern edge of the Dogger Bank. The positions from which measured samples were taken on the two voyages are shown in Text-Figures

1 and 2. The measurements for each length unit are plotted on the charts near the appropriate station and the dotted outlines of the patch on each cruise show the supposed direction of drift. The position shown in Text-Figure 1 is nearer the colder northern water and those in Text-Figure 2, successively further away from this origin. The temperatures at different depths for the three stations considered show the degree to which this was the case. But it is the origin of the water masses rather than the temperature differences which are important.

	Cr. H. Stn. Q (Fig. 1)			Cr. J. Stn. 26 (Fig. 2)			Cr. J. Stn. 20 (Fig. 2)	
m.	°C.	Salinity	m.	°C.	Salinity	m.	°C.	Salinity
0	12·23		0	12·21	34·67	0	12·42	34·78
10	12·23	34·43	20	12·34	34·71	20	12·44	34·64
30	12·23					40	12·43	34·92
50	12·23							
70	12·19							

Bearing these observations in mind it is interesting to note that the cell diameters of the subsequent and warmer samples show an increase in the following progression of their means :

Cr. H.	Stn. Q.	15·3	(14-10-32)
Cr. J.	Stn. 26	16·0	(29-10-32)
Cr. J.	Stn. 20	16·8	(28-10-32)

The increase is also apparent from an inspection of the diameter frequencies plotted in Text-Figures 1 and 2.

1933.

In this year samples of Rhizosolenia from populous or relatively populous catches were measured for July and September as well as October. All the samples are referable to patch areas of this diatom whose drift and growth are elsewhere discussed (Savage and Wimpenny [**17**]). The results are shown in Table II. The July and September samples came from a position near the South-West Patch of the Dogger Bank. Both of these samples seem bimodal at about 12 and 20 units, but while in September the values were rather evenly distributed, in July the majority were grouped around the mode with the lower value. The July Rhizosolenia were therefore narrower, the mean being 13·6 units compared with 16·7 in September. The corresponding surface temperatures had meanwhile increased from 13·58 in July to 15·78° C. in September.

The four samples from each of the October cruises all showed the same tendency to be bimodal that has already been referred to. With the exception of Station 28, Cruise K, and Station 35, Cruise L, the mode at the higher of the two values (*circa* 20 units) was the dominant one and the mean diameters were greater than in the September sample. Stations 28, Cruise K, and 35, Cruise L, consisted mainly of diatoms with narrower diameters and though the water at Station 35, Cruise L, was actually warmer (14·08° C. at surface) than that at another station on the same cruise where the diatoms were wider (Station 30, 12·64° at surface), both stations lay in the track of water entering the S.W. North Sea from the thermocline area in the north.

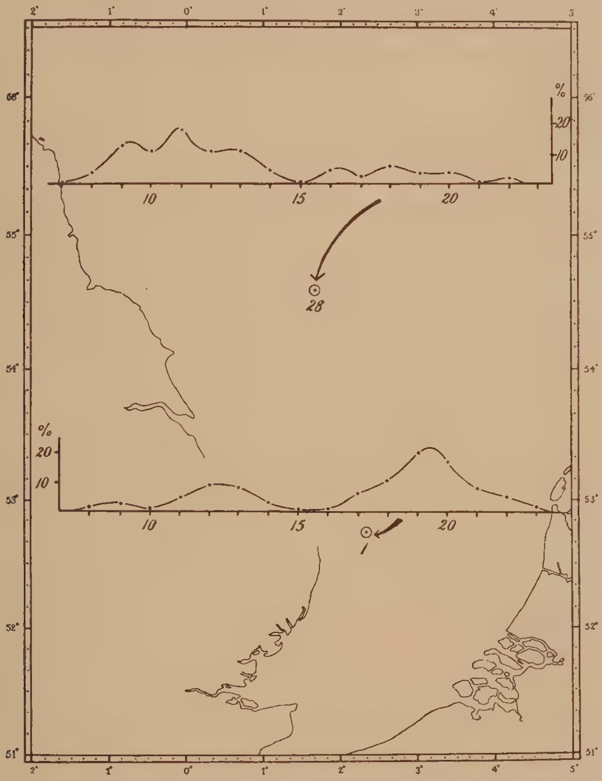

Fig. 3.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 1 and 28 of cruise K, October 1933.

The diameters of the Rhizosolenia typical of the north and south parts of the area discussed are shown graphically for the two October cruises in Text-Figures 3 and 4, where the positions of the stations are also given. If we compare the measurements for October, 1933 with those of the previous year (Figs. 1 and 2 with 3 and 4 and Table II) we see that in 1933 there were more wide diatoms. It may also be added that the species spread further south.

1934.

Though only nine samples were measured in this year, they were more widely spread in time. The first sample was taken from a light patch found off the N.E. coast in May, which was believed to be moving in the Firth of Forth Swirl (cf., Tait [**15**], Savage and Wimpenny [**17**]). The outline of the patch, the position of the station from which the sample was obtained and a diagram showing the frequencies at the different diameter units are shown in Text-Figure 5. It is clear that there is a peak in the measurement scale in the neighbourhood of 10–11. Another series of measurements was taken in June from what was thought to be the same patch system, together with a sample from a different population in the

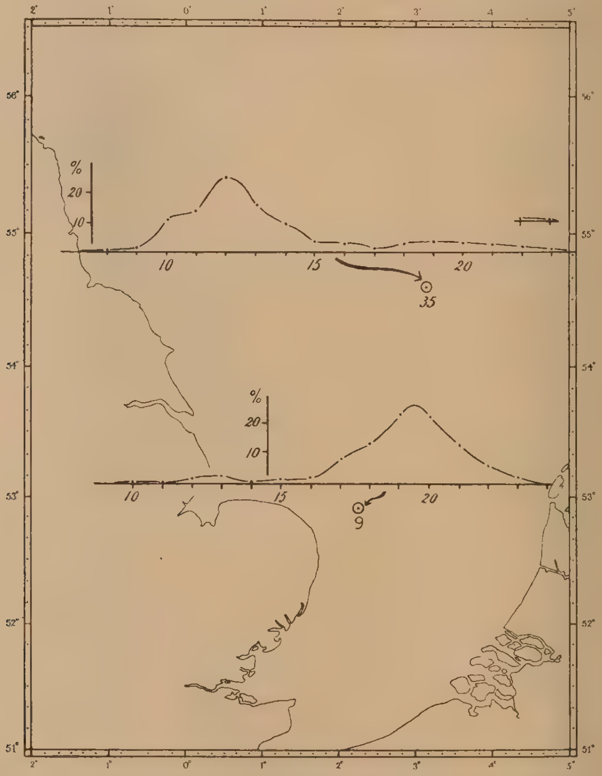

Fig. 4.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 9 and 35 of cruise L, October 1933.

neighbourhood of the S.W. Patch of the Dogger Bank and probably near or under the influence of the S.W. Dogger Swirl. The surface water in the northern patch was 11·33° C. compared with 7·60° C. the month before and the main group of measurements had a mode between 11 and 12. There were also indications of another group of diatoms at a diameter of 18 units. The increase in size of the principal group is slight and may be unreal, but in view of the other occasions in which increase in size parallels increase in temperature, I feel bound to draw attention to it here. The principal mode found in the Firth of Forth area was absent from the sample taken on the S.W. Dogger Bank and, as will be seen from an inspection of Text-Figure 6, the diameter values were rather evenly grouped around 17–18. The mean size of this sample was 17·02 compared with 11·89 from the one further north. The temperatures and salinities

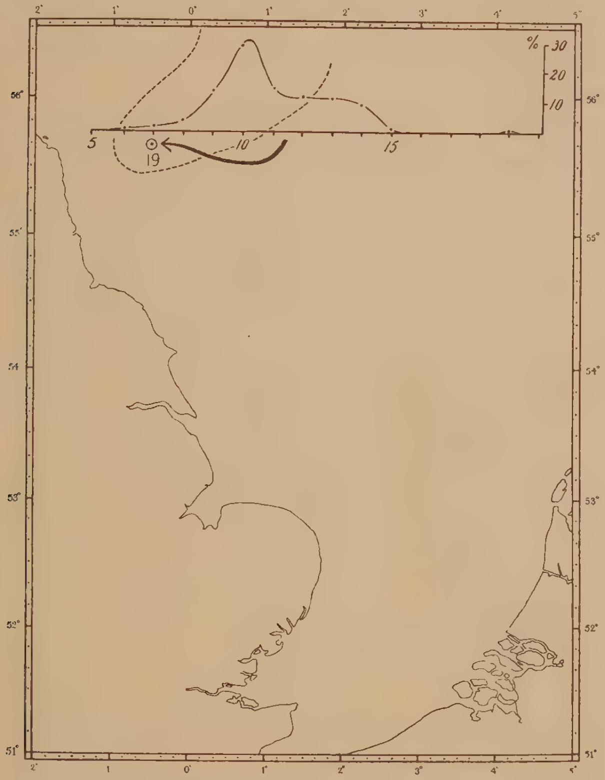

Fig. 5.—The percentage of *Rhizosolenia styliformis* cells at different diameters from station 19 of cruise C, May 1934. The area of a patch of this diatom is shown by a dotted line.

throughout the water column for these two stations show that the southern one was actually hotter and less salt than a comparison of surface values would make it appear.

	Northern Station (E 5)		Southern Station (E 17)	
	T.°C.	Salinity	T.°C.	Salinity
0	11·33	34·97	11·46	34·79
10	11·32	35·02	11·36	·79
20	9·39	·00	10·66	·79
30	8·01	·01	10·58	·78
40	7·59	·01		
60	7·57	·00		

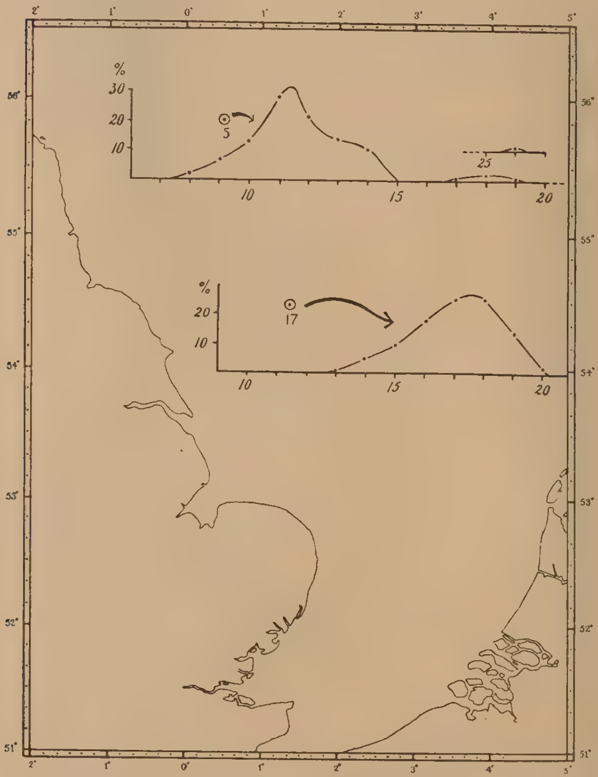

FIG. 6.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 5 and 17 of cruise E, June 1934.

Samples from the S.W. Dogger Bank area are available for July (G5), September (L17), October (M14), and December (Onaway 35 station 6). In July and September the wide diatoms only were present (Table II).

The mode decreased slightly from June onwards though the mean rose to 17·39 and thence fell to 16·15, 15·86 and 15·75, the corresponding surface temperature being 11·46, 15·39, 16·33, 13·04 and 10·93°C. At the end of the year and in October the wide cells are not so homogeneously distributed around a mode and the greater number of cells in these months lies between 15 and 17 units of diameter. The diameters for three stations in October are shown in Figure 7. Station 14 near the S.W. Patch of the Dogger Bank has already been referred to and Station 21, N.E. of the Frisian Islands, is seen to be generally similar, though the surface temperature is much higher (13·04 and 15·13) and the salinity 0·2°/₀₀ lower. The remaining position, Station 3, is near that shown in Figure 5 and described as likely to be in the Firth of Forth Swirl. The diatoms from this station fall into two groups, one centred around measurement units 15–17 and the other having a mode at 7–8. The smaller group is similar to that found in May except that the mode has moved back 3 units. The large group is generally similar to those further south. In spite of the small group the mean diameter of the diatoms present at this northern station in October was 12·50 compared with 10·94 in May. In the meanwhile the surface temperature had risen from 7·60°C. to 11·42°C. and the salinity had declined 0·1°/₀₀. Conditions throughout the water column were uniform at the May station but in October this was not so as the following list of temperatures and salinities will show.

Depth (m.)	Cr. C. Stn. 19 (May) T.°C.	Salinity	Cr. M. Stn. 3 (October) T.°C.	Salinity
0	7·60	35·03	11·42	34·89
10			11·38	34·90
20	7·58	35·05	11·32	34·90
30			11·16	34·93
40	7·56	35·05	10·31	34·97
50			9·98	35·09
60	7·43	35·01	9·67	34·94
100			9·11	35·11

Conditions below 40 m. in October approach those of May and it may be that there is some selective distribution of the different sizes of cell throughout the water column. Samples taken at different depths in the Southern Bight do not show any marked differences in size but in these cases the water was nearly uniform in temperature and salinity from top to bottom.

Relation of Size to Temperature.

Of the years 1932–34, 1933 was the year in which the highest temperatures and salinities and the greatest production of *Rhizosolenia* *styliformis* were found in the area we are discussing (Savage and Wimpenny [**17**]). In this year the largest diameters were met with. Also, within each year there was a seasonal difference in size which we have seen may be broadly related to temperature. Below I give a list showing the mean measurements of my series of samples and corresponding temperatures and salinities at 20m.

Cruise	Station*	Date	Mean Size	T.°C. at 20m.	Salinity at 20m.
1932					
H	Q.	14–10	15·30	12·23	34·43
J	20	28–10	16·78	12·44	34·64
J	26	29–10	16·01	12·24	34·71
1933					
F	5	13–7	13·60	13·64	34·74
J	5	19–9	16·70	15·60	34·71
K	1	7–10	17·10	16·34	34·56
K	12	9–10	19·00	15·28	34·70
K	13	9–10	17·60	15·51	34·72
K	28	13–10	12·80	14·59	34·81
L	9	18–10	18·92	14·96	34·56
L	15	19–10	17·40	14·89	34·88
L	30	21–10	18·04	12·64	34·76
L	35	22–10	13·35	14·08	34·85
1934					
C	19	21–5	10·94	7·58	35·05
E	5	15–6	11·89	9·39	35·00
E	17	17–6	17·02	10·66	34·79
G	5	18–7	17·39	14·08	34·79
L	17	22–9	16·15	16·33	34·87
M	3	7–10	12·50	11·32	34·90
M	14	9–10	15·86	13·04	34·71
M	21	10–10	15·75	15·15	34·66
Onaway 35	6	20–11	15·75	10·93	–

The correlation coefficient with temperature is +0·59 and with salinity —0·59. It seems likely that these relations have some significance, for the correlation values just quoted would only arise in a chance manner less than once in a hundred times.

Change in diameter is well known to take place in diatoms (cf. Fritsch [**3**]). At each division the cell becomes slightly smaller. In the course of time the cell becomes much smaller and an auxospore is formed producing very much wider daughter cells which in turn commence to divide and diminish in size. The diminution in size appears to be slow but the increase is of course sudden. Schütt [**13**] who has described the auxospore formation of *Rhizosolenia alata* in the Baltic, found the change in mean diameter between November–December, 1884, and March, 1885, as 5·49μ to 5·41μ. In August 1885 the mean diameter was 3·34; the auxospores producing a generation at 9·35 which had diminished to 8·32 by September.

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* The station numbers of the different cruises do not necessarily correspond.

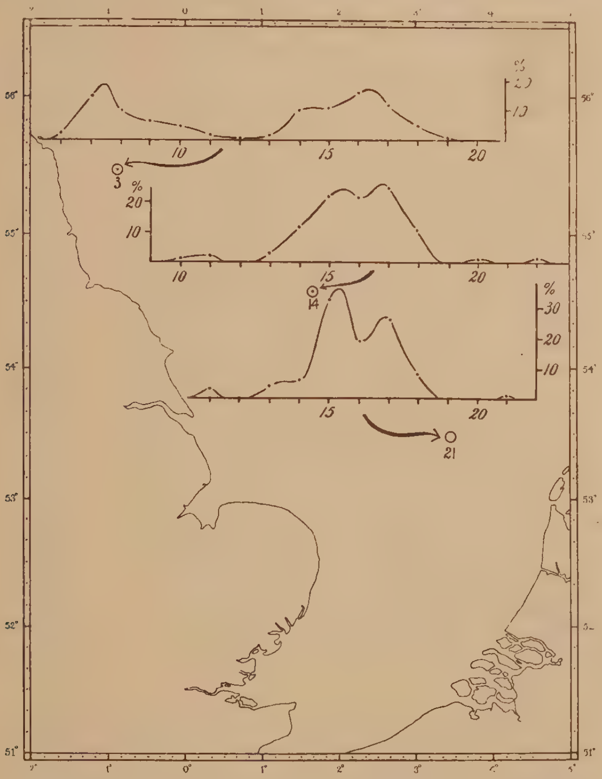

Fig. 7.—The percentage of *Rhizosolenia styliformis* cells at different diameters from stations 3, 14 and 15 of cruise M, October 1934.

Schütt considers that auxospore formation in this species takes place in August–September each year. The auxospores of *Rhizosolenia styliformis* have been described by Gran (**4**), who found them in August–September, 1900, between north Norway and Bear Island and also between 4½° and 3½° W Longitude at about 70½° N Latitude. In this case the mother cells measured 22–25 and the auxospore 100—figures similar to the smallest and largest dimensions mentioned in this paper. Auxospore formation in these two cases, it will be noted, fell at the warmest time of the year. No auxospores were seen during examination of the material discussed here, but the largest sized diatoms dominant in 1933 must have had this origin. Whether the warmer sea temperatures of the Southern Bight had anything to do with auxospore formation one cannot say definitely, but the fact that auxospore formation in the genus occurs at the warmest season makes one think that a warmer year might be especially favourable to it.

Of a progressive diminution of size due to cell division the data affords several examples. A comparison of Text-Figure 1 with Text-Figure 3 suggests that a small group in 1932 had become smaller in 1933. Similarly the large group of October, 1933, seems to be identical with a smaller group in 1934 (compare Text-Figs. 3 and 4 with 7). Finally in 1934 there is a decrease in size of what appears to be the same small group found off the N.E. coast between May and October and a decrease in modal size throughout the year for the larger group found in the neighbourhood of the S.W. Patch of the Dogger Bank.

Apart from auxospore formation and the continuous reduction of size due to cell division there is a survival of larger individuals, even in populations whose modes are growing smaller, which seems likely to be related to increase of temperature. This apparent selection of the wider cells as the patch drifted into areas of higher temperature is shown by comparing the diameter distributions for October, 1932, given in Text-Figure 1, with those in Text-Figure 2 which show conditions a fortnight later. On the later October cruise itself, the sample taken in the warmer part of the patch shows a continuation of this effect when compared with a sample from a cooler part. Again, in 1934, the large group found in the S.W. Dogger Bank neighbourhood increased in average size between June and July parallel to the rise of temperature, although the mode showed a decrease (Table II). In both these cases temperature and salinity rose together.

On the whole, therefore, I am inclined to think that it is increase in temperature rather than decrease in salinity which may operate in a selective way by favouring the larger individuals of a normal strain of cells in a manner discussed later, and possibly by stimulating auxospore formation at a larger size. The general correlation with decreasing salinity is due, perhaps, to the special conditions of the area where the main river outflow and shallower water is found in the warmer south. If this is so the correspondence between small diatoms and high salinity would be fortuitous.

The Relation of Length to Diameter in *R. styliformis*.

In Text-Figure 8 I have plotted the diameter of 100 cells from Station 35 Cruise L, 1933, against their length measured from the base of each cell "beak" and not from the tip of the "beak" itself. It will be seen that the cells increase little in length with increasing diameter, nevertheless they do not diminish and so the cells with bigger diameters are in fact bigger cells. The whole question, however, needs a wider investigation.

RHIZOSOLENIA ALATA.

During a cruise made between October 5–15, this species was met with over a considerable area of the S.W. North Sea and at several stations it was noticed to be in the process of forming auxospores. The distribution is shown in Text-Figure 9 where its presence is denoted by a cross and its absence by a dash. Those stations at which auxospores were seen are indicated by a circle round the cross. The southern limit of the area in which the surface water was still cut off from the bottom water by a sharp temperature difference is shown by a strong dashed line. It will be seen that auxospore formation did not take place within the thermocline area but on its edge, where the layering had broken down and where vertical mixing was taking place.

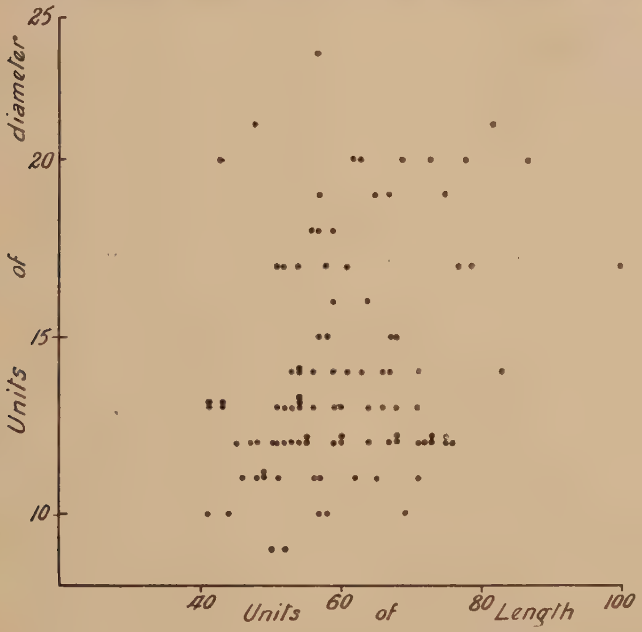

FIG. 8.—The diameter plotted against the corresponding length for 100 cells of *Rhizosolenia styliformis* taken at station 35, cruise L, 1933.

The diatom only occurred densely at Station 8, a position about

30 miles N.E. of Scarborough. Here it appeared to be multiplying briskly and of 50 cells measured for diameter no less than 9 were forming auxospores.

The auxospore of *R. alata* has been well described by Schütt (**13**) and the abundant material from my Station 8 is in agreement with his descriptions. Commonly-met stages are reproduced in the photomicrograph of Plate I, as well as in the drawings of Text-Figure 10. There is a difference in the relation of the size of the original cell to the auxospore between my material and that which Schütt collected in the Baltic in August, 1885, which is worthy of note. This is that whilst in my material the auxospore

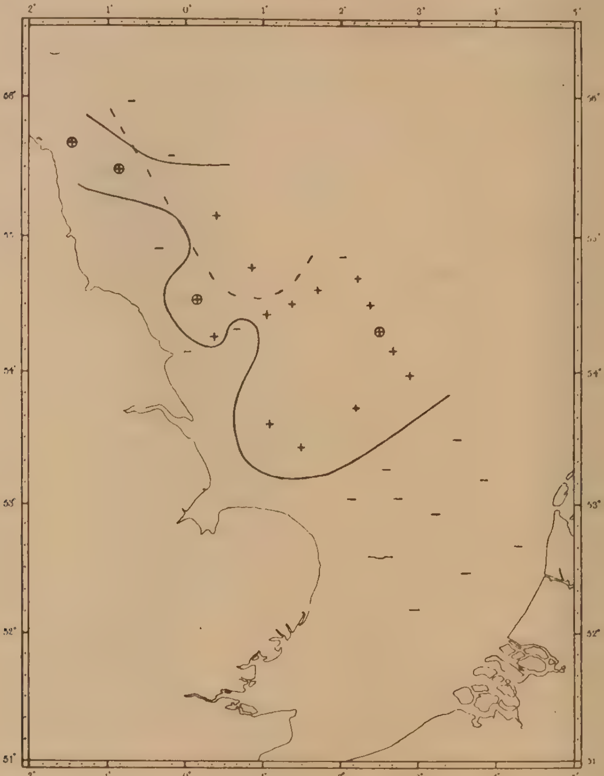

Fig. 9.—The stations of cruise M, October 5–15, 1934. The presence of *Rhizosolenia alata* is denoted by a cross, its absence by a dash. Where auxospore were present the cross is surrounded by a circle. The dotted line indicates the southward and westward limit of the thermocline area and the whole area of distribution is bounded by a continuous line.

diameters represented a fourfold increase from approximately 4 to 16μ, Schütt's comparable increase was threefold—from 3 to 9.

The fifty individuals constituted a random sample of Station 8. Their diameters in μ are given in Table III and are expressed graphically in Text-Figure 11. In this figure the free cell diameters are plotted above the abscissa, whilst below these are expressed the two diameters of each auxospore-forming individual. The wide auxospore diameters are on the right of the diagram and have been distinguished by blackening the area of their distribution curve. The diameters of the original cell to which they belong have been indicated by figures in brackets. The ordinates above and below the line express the results as a percentage which, of

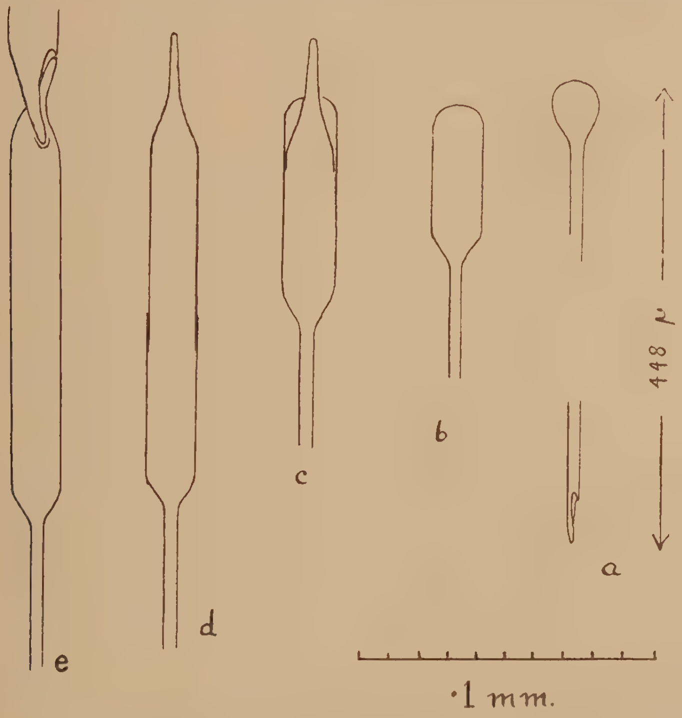

Fig. 10.—Different stages in the development of the auxospore of *Rhizosolenia alata*.

(*a*) Auxospore, a spherical capitulum, newly formed at broken end of mother-cell.
(*b*) Auxospore capitulum extending as cylinder of increased diameter.
(*c*) New calyptra formed within cylindrical auxospore and rupturing distal wall.
(*d*) Cell having extended in length and resulting in primary increasing cell of wide diameter.
(*e*) Primary increasing cell having divided to produce secondary increasing cell and new wide cell of the daughter generation.

course, does not take into account the black areas. Below I give the individual measurements in μ of the nine auxospore-forming cells of this sample.

Diameter of original cell	Diameter of auxospore
3	12
4	15
4	16
4	16
4	16
4	16
4	16
4	18
5	15

It will be seen that at Station 8, Cruise M, the sample consisted mainly of very narrow cells a considerable proportion of which were forming auxospores. Samples of a hundred cells of the same diatom from each of two stations further to the south and from the same cruise have been similarly measured. The results are shown in the table and figure already mentioned. In these cases there were neither auxospores nor any of the very thin cells, the majority being in the neighbourhood of 12μ in diameter and likely, therefore, to be related to the auxospore generation whose formation was taking place further north.

The general water movements in the area covered by Cruise M, 1934, have been discussed elsewhere by Savage and Wimpenny (**17**). According to these deductions the water from Station 8 would be moving to Station 17 and turning thence to Station 15. In this case it would be easy to understand that the auxospore generation formed at Station 8 with a diameter of about 16μ would drift southwards, continuing its division and so reducing its size to the mode at about 12μ. If this account of the water movements is correct, it would however be expected that the diameters at Station 15 would be rather smaller than those at Station 17. An inspection of Figure 11 shows that in fact this is not the case and that the cells at Station 15 were on the whole wider than those at Station 17. In these circumstances it is worth while to inquire into factors which

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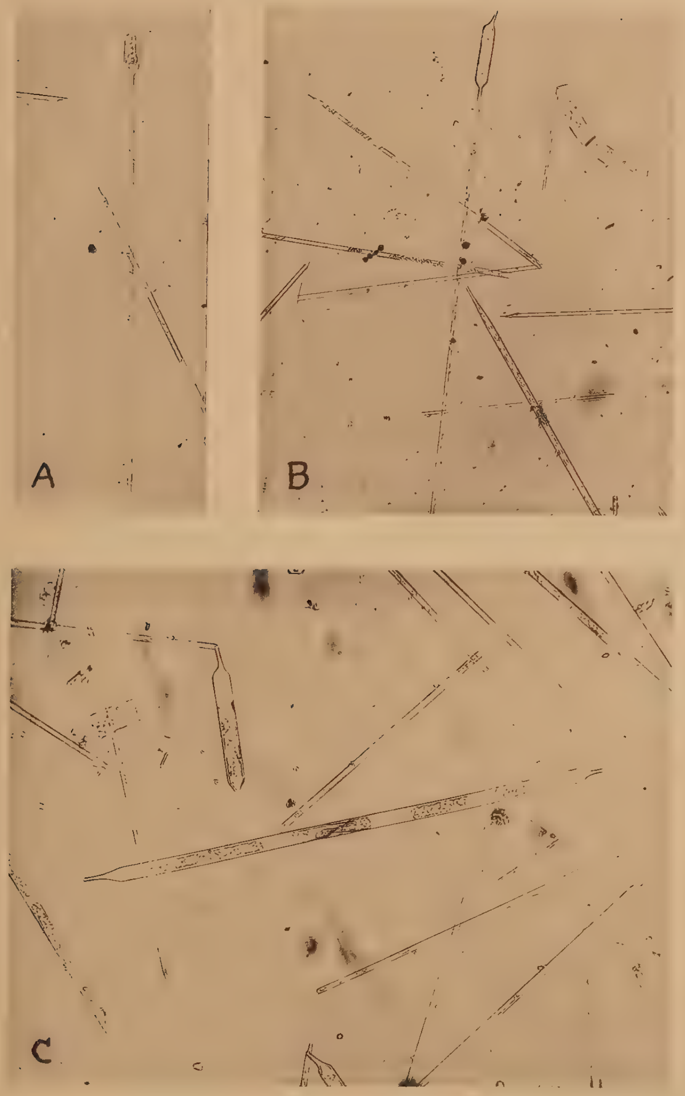
PLATE I.

Photomicrographs of *Rhizosolenia alata* during and after auxospore formation. Magnification × 100.

A. Auxospore newly formed from mother-cell. B. First cell of increased size arising from the auxospore. C. Newly formed thick daughter cells in process of division.

PLATE I.



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might cause a size selection. Temperatures and salinities at different depths at each of the three stations are available and I give them below :

Depth	Station 8		Station 17		Station 15	
m.	T.°C.	S.°/₀₀	T.°C.	S.°/₀₀	T.°C.	S.°/₀₀
0	11·04	34·74	13·98	34·64	15·15	34·95
10	11·00	34·79	13·99	34·72	15·18	34·76
20	10·96	34·74	14·01	34·71	15·16	34·75
30	10·63	34·79			15·17	34·76
40	9·66	34·81			15·17	34·78
50	9·63	34·74			15·17	34·73
60	9·63	34·78				

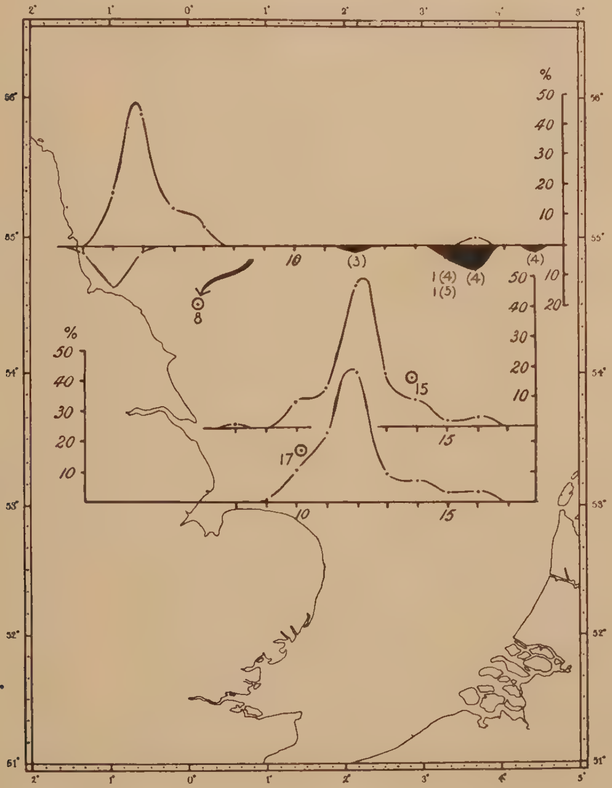

FIG. 11.—The measured diameters in μ for 100 individuals of *Rhizosolenia alata* from stations 15 and 17 and for 50 individuals from station 8 of cruise M, October 5–15, 1934. For station 8, the diameters of the cells of the old generation are plotted above the abscissa, whilst below are plotted the two diameters of each auxospore-forming individual. (See also text.)

The thin sample occurred at the station of lowest temperature and for the two stations from which the new generation came it will be seen that the temperature was higher at the station where the cells were of slightly greater diameter.

The salinity does not show any relation to the question of size, for though it decreases from Station 8 to Station 17 whilst there is an increase of diameter, from Station 17 to 15 there is an increase of both diameter and salinity.

THE DIAMETERS OF PELAGIC MARINE DIATOMS IN GENERAL.

The emergence of a relation between temperature and cell diameter in Rhizosolenia, whether causal or not, was surprising and unexpected, particularly so in view of the fact that copepods and other zooplankton forms so often diminish in size at higher temperatures.

It therefore seemed useful to examine the size of other pelagic diatoms according to their geographical distribution as a whole and the distribution of species and varieties of the same genera.

Of all diatoms *Ethmodiscus gazellæ* appears to be the largest, the diameter being given by Castracane (**1**) as 1600μ. This species comes from the warm Atlantic waters near the Cape Verde Islands. Arctic and Antarctic seas do not appear to possess very large diatoms which would appear to be restricted to warmer seas. Small diatoms on the other hand appear to be found in both warm and cold seas, though I hope to show later that more small species are found in the colder seas. It is difficult to say which is the smallest diatom, but it is probable that the Arctic *Chætoceros filiformis* with a diameter of 3μ is a strong candidate for this record. Using the diameter as the measurement in common use is convenient but it is misleading on occasions. For instance, in the genus Thalassiothrix, the cold-loving species is long and hairlike, this length representing the diameter. Actually the cell is so extremely thin owing to its diminutive true length that it is possibly less bulky than its southern congeners. For reasons of which the case just quoted is an extreme example, it is not possible to say with the data available which is the smallest marine diatom.

A consideration of the diameters of species and varieties of the same genus allows us to draw a more definite deduction on the relation of small size to distribution in colder seas. In Table IV I have taken an arbitrary list of species and varieties of which there are more than one in a given genus, and set down their diameters according to their geographical distribution. The list is taken from Dr. Lebour's *The Planktonic Diatoms of Northern Seas* (**8**), and the species appear in the order set down in that book. Most of the diameters appear in the work just quoted but in some cases where they do not appear in the book I have been able to obtain them from other authorities, particularly Gran (**5**). The two species of the genus Skeletonema have been omitted as they both appear to be cosmopolitan. The geographical distribution follows the division made by Ostenfeld (**10**) except that I have divided the group "Temperate neritic" into "North temperate neritic," "Temperate neritic" and "South temperate neritic." In the interests of brevity I have also regarded the small number of littoral and tychopelagic species as neritic. This analysis has been condensed into four groups of genera, which are given below :

Genera showing species of smallest diameters in cold areas.	Genera showing species of smallest diameters in warm areas.	Genera showing species of largest and smallest diameters in cold areas.	Genera showing* species of largest diameters in cold areas.
Melosira	Lauderia	Schröderella	Biddulphia
Coscinodiscus	Leptocylindrus		Thalassiothrix
Chætoceros	Bacteriastrum		
Rhizosolenia			
Thalassiosira			
Stephanopyxis			
Fragilaria			
Asterionella			
Achnanthes			
Navicula			
Nitzschia			
Actinoptychus			
Asteromphalus			

Out of the nineteen genera whose distribution could be dealt with it will be seen that in thirteen of them the species with the smallest diameters come from the colder part of their assumed area of distribution, and in only three genera do the smallest species come from the warmer part of the generic range. For the latter group it is possible that narrower cells of the warm water Lauderia and Bacteriastrum actually represent bulkier cells, as their length is much greater than in the wider species. One genus has its largest and smallest diameter in cold areas and in the last group there are two genera having their widest species in cold areas. One of the genera of this group, Thalassiothrix, has already been discussed, and in the case of Biddulphia the reference of the genus to this group and not to the majority group

* Owing to the number of possible combinations this column does not coincide with column 2 as might be expected.

depends upon the inclusion of *Biddulphia arctica* which is a littoral and not truly planktonic species. This series of species known to workers in the North Temperate zone may, therefore, be taken to show a correspondence between small diameters and cold areas.

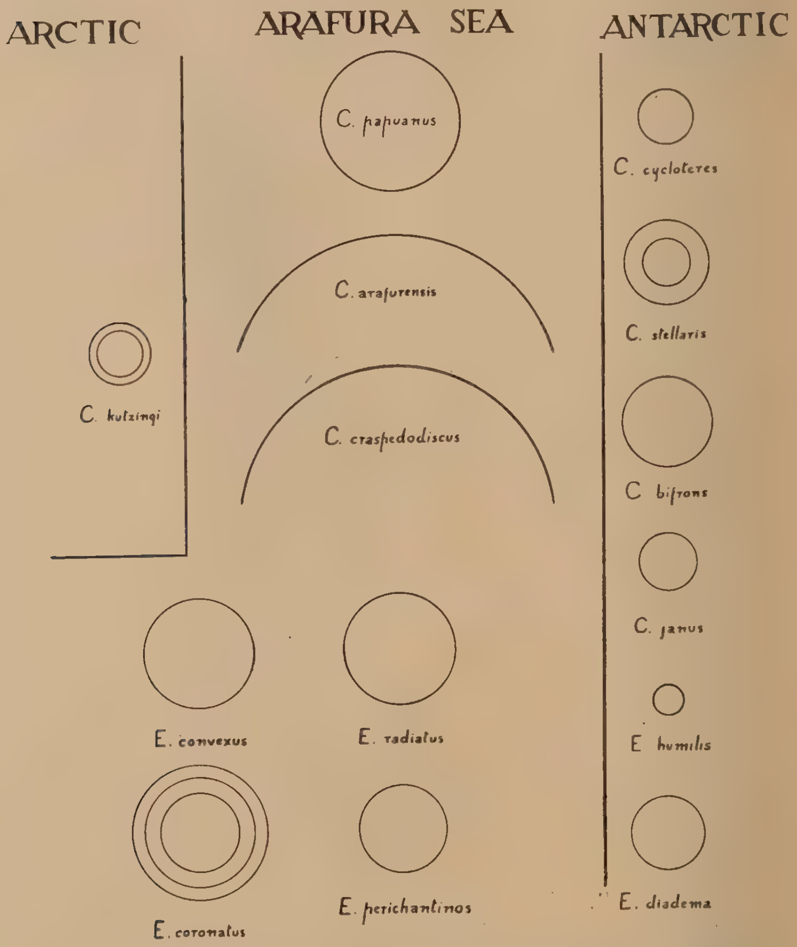
ARCTIC
ARAFURA SEA
ANTARCTIC
C. papuanus
C. arafurensis
C. craspedodiscus
C. kutzingi
C. cycloteres
C. stellaris
C bifrons
C. janus
E humilis
E. convexus
E. radiatus
E. coronatus
E. perichantinos
E. diadema

FIG. 12.—Valvar aspect of all species of Coscinodiscus and Ethmodiscus figured in the Challenger Report on diatoms, as coming from the Arctic, the Arafura Sea, and the Antarctic. Where several diameters are given for one species these diameters represent different varieties. Castracane's nomenclature has been retained.

I have attempted to work out another "random" sample to test the supposed relation between diameter and low temperature, by drawing all the members of the genera Ethmodiscus and Coscinodiscus that

Castracane has figured in the Challenger Reports (**1**) as having come from three areas—the Arctic, the Antarctic and the Arafura Sea in the East Indies. These diameters appear in Text-Figure 12 and it will be seen that the smallest of them come from the colder areas in the case of each species.

The following measurements in μ of the extreme diameter values for six genera common to three areas investigated by the "Valdivia" Expedition afford similar evidence :—

	Arctic Ocean	Atlantic Ocean	Indian Ocean
Coscinodiscus	14–280	30–1074	32–544
Asteromphilus	22–136	88	90–180
Actinocyclus	32–124	112–232	26
Dactyliosolen	6–88	22–45	10–28
Rhizosolenia	5–278	10–400	12–272
Fragillaria	6–12	42	50

DISCUSSION.

In the earlier part of this paper it has been shown that there are changes in the diameters of *Rhizosolenia styliformis* cells found in the North Sea, and that these changes are related to spatial and seasonal distribution in such a way as to suggest that temperature is an important influence. The result of experiences in the North Sea would lead one to expect large Rhizosolenia cells at high temperatures, and low salinities. Later the general question of cell diameter in marine diatoms was considered, and evidence was brought forward to show that within the limits of certain available information there is a tendency for the species or variety that has the smallest diameter to be found in the coolest part of the generic range. The tendency for diatom size to increase with temperature is thus a deduction common to both sections of the work. The connection with salinity would, however, seem less consistent. Whereas the relation between Rhizosolenia size and salinity in the North Sea would suggest a similar inverse one for diatoms generally, it is in fact found that as salinity tends to be higher in the warmer seas, the general relation between diatom size and salinity appears to be a direct one. On account of this inconsistency and on account of the consistency of the temperature relation, I am inclined to think that temperature stands in the more significant relation to diatom diameter.

Let us, therefore, consider the effects that an increase or decrease of temperature might be expected to have on a diatom cell postulated to be floating in equilibrium with its medium, or of diatom cells of the same species suddenly transported to warmer or cooler seas.

1. There would be a tendency for increase in the salinity due to increase

of temperature, which by causing a rise in the specific gravity of the sea water, would cause the cell to rise or would allow a larger cell with relatively less surface to float whereas formerly it would have sunk.

2. The viscosity of sea water decreases with rise of temperature. According to Ostwald (**11**) this importantly affects the suspension of plankton organisms. Hence a rise in temperature would cause our diatom to fall and would only support a diatom having a greater surface compared with its volume, that is to say a smaller diatom of its own shape.

3. An increase or decrease in temperature increases or decreases the rate of respiration, but it does not follow that this rise will accelerate or diminish assimilation at an equal rate. Indeed, there is some experimental proof that respiration increases more rapidly than photosynthesis with a rise of temperature for *Fucus* (Kniep [**7**]). In this case a temperature rise might cause respiration to overtake assimilation and cause the death of the diatom. On the other hand a larger diatom with a surface relatively less compared with its volume and a lower metabolic rate to start with, might be able to sustain its vital metabolism. As the division rate of the larger species of diatom is lower than that of the smaller a lower metabolic rate in larger diatoms seems likely.

4. Calcium in the form of its carbonate and bicarbonate is more soluble in cold water. A rise of temperature would therefore mean a little less available calcium. In the open sea Wattenburg (**18**) has proved that there is less dissolved calcium in the warmer parts. According to Pearsall's views (**12**) the presence of calcium tends to cause the earlier wall-hardening in *Ceratium hirundinella* and so reduces the size of the cell. The differences in calcium content found by Wattenburg were, however, so small that it is not thought likely that the cell walls of marine diatoms would be noticeably affected.

5. Consider our postulated diatom in its newly-formed auxospore stage. At this time the auxospore is a protoplast surrounded by a thin pellicle and it seems likely that with a rise of temperature the surface tension would be less and the auxospore would therefore assume a larger size.

Changes in specific gravity corresponding to salinity changes are likely to be inconsiderable and might in any case be offset by osmotic effects. For this reason I am not inclined to think the effect important. It should be noted, however, that it would encourage the larger diatoms in the hotter seas if it operated appreciably.

The second consequence works in a direction contrary to all others, in that it would favour smaller diatoms in warmer water. According to Ostwald the viscosity of sea water falls about 2% for each degree rise in temperature and, other things being equal, a passively floating organism would have to increase its surface compared with its volume to keep floating as the temperature rises. This may be done by the development of specially formed organs or by a diminution in size for organisms of the same shape. The work of Steuer (**14**), Marshall (**9**) and Bogorov (**2**) suggests that diminution of size with rise in temperature is broadly true for the copepods of the zooplankton. For diatoms the balance of the evidence in the present paper indicates increasing size with rise of temperature, and for this reason it is a matter of some importance to note that the opinions expressed by Professor Gran cannot be urged in support of such a generality. Gran (**6**) says that a number of species show winter and summer or hot water and cold water varieties, in which the summer and hot water forms have a more slender structure and thinner walls, though at the same time their surface is comparatively larger. The more slender types of *Chætoceros decipiens* found in summer and in the warmer parts of its range, other species of Chætoceros, and *Biddulphia aurita* are cited as examples. A viscosity effect cannot, therefore, be dismissed and may explain some cases but cannot, I think, do so for the majority of diatoms.

The remaining possibilities are largely speculative but it is possible that they all fit the facts and are all involved. The effect of temperature on respiration seems to me the most likely way in which temperature might affect diameter by a selection of the larger cells as it rises. Surely, as temperature rises respiration must be increased, but assimilation may not be able to increase as the needs for it are at times lacking. Now, if the general metabolism, including respiration and assimilation, proceeds in proportion to the relation of surface to volume, those cells with the greatest relative surface—the smallest—will be the first to be adversely affected by a rise in temperature. This selection should take place rather more rapidly than the last two effects, and it is interesting to see, on pages 37, 40 and 46 above, the evidence of a gradual selection in size of Rhizosolenia between months and running parallel to the temperature. This apparent selection is particularly interesting between June and July, 1934, where, though the mode shows that the stock is proceeding to get smaller, as a characteristic diatom stock undergoing division must do, the actual mean size is increased as a result of the greater numbers of wider diatoms. The respiration-size effect would be difficult to try out by an *in vitro* experiment, but it seems possible that Pearsall's wall-hardening theory may be dealt with in this way, using very small differences in calcium content, such as are found in the sea. The possibility of there being variations in the size of auxospore on first formation should be cleared up as a result of continued observations at sea, but up to the present there are no indications of wide differences in size, my observations in the southern North Sea in 1932–3 agreeing fairly well with those of Gran made in the Norwegian sea in the summer of 1900.

SUMMARY.

1. The diameters of samples of *Rhizosolenia styliformis* taken in the S.W. North Sea between 1932 and 1934 revealed the presence of large and small populations. The largest diatoms were found in 1933, in which year, or late in 1932, it was thought that auxospore formation might have taken place.

2. The large and small groups mentioned in (1) gave indications of a continuous diminution of size judging by an inspection of their modes. Notwithstanding this there appears to have been some selection of the larger cells, as the whole samples tended to increase in size with a rise of temperature.

3. The correlation coefficient between the temperature at 20m. and the mean diameters was 0·59. That for salinity in the same circumstances was —0·59. The inverse correlation with salinity is thought to be due to the topography of the area.

4. Auxospore formation in *Rhizosolenia alata* was observed on a cruise in October 1934, and was seen to be the cause of a large and small generation in the plankton.

5. Evidence is produced showing that in general the widest diatoms with the largest diameters come from warmer areas and the smallest from cold ones. In this case the relation with salinity would be direct and not inverse as was the case with *Rhizosolenia styliformis.*

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TABLE I.

DATES AND POSITIONS OF STATIONS FROM WHICH RHIZOSOLENIA MEASUREMENTS WERE MADE.

Cruise.	Station.	Date.	Latitude.	Longitude.	No. measured.
H	Q	14/10/32	54° 05′	1° 34′ E.	100
J	26	29/10/32	53° 45′	3° 20′ E.	100
J	20	28/10/32	54° 10′	4° 45′ E.	100
F	5	13/7/33	54° 30′	1° 20′ E.	100
J	5	19/9/33	54° 27′	1° 21′ E.	100
K	1	7/10/33	52° 44′	2° 19′ E.	100
K	12	9/10/33	53° 33′	1° 21′ E.	203*
K	13	9/10/33	53° 50′	2° 02′ E.	100
K	28	13/10/33	54° 35′	1° 40′ E.	100
L	9	18/10/33	52° 55′	2° 15′ E.	300
L	15	19/10/33	53° 19′	3° 07′ E.	299
L	30	21/10/33	54° 17′	1° 42′ E.	300
L	35	22/10/33	54° 36′	3° 08′ E.	295
Onaway 25	8	10/11/33	15′ N.N.W. “ Tea Kettle Hole ”		102
,, 25	9	10/11/33	“ Tea Kettle Hole ”		300
,, 29	“ Tea Kettle Hole ”	1/12/33	“ Tea Kettle Hole ”		100
C	19	21/5/34	55° 40′	0° 29′ W.	100
E	5	15/6/34	55° 51′	0° 31′ E.	100
E	17	17/6/34	54° 29′	1° 22′ E.	100
G	5	18/7/34	54° 14′	0° 21′ E.	100
L	17	22/9/34	54° 29′	2° 23′ E.	100
M	3	7/10/34	55° 28′	0° 53′ W.	100
M	14	9/10/34	54° 35′	1° 41′ E.	100
M	21	10/10/34	53° 28′	3° 27′ E.	100
Onaway 35	6	20/11/34	54° 28′	1° 41′ E.	100

* 100 Hensen, 103 in tow-net at 10m.

TABLE II.

MEASUREMENTS OF *Rhizosolenia styliformis* (DIAMETERS).

Figures denote % frequencies. Top row measurement units.

1932 : Cruise H Hensen haul and Cruise J surface tow-nets.

Cruise.	Station.	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
H	Q	2	3	3	4	9	16	11	11	10	3	3	11	4	3	3	2	1	1
J	26		1	2	3	9	14	14	10	9	9	2	4	8	4	7	1	2	1
J	20				2	6	6	8	12	12	17	9	7	9	8	3	–	1	–

1933 : Hensen hauls.

Cruise.	Station.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
F	5	1	4	7	6	9	20	18	5	6	5	2	1	3	4	5	3	–	1
J	5			2	8	9	10	5	4	3	1	5	4	14	8	13	5	9	
K	1		1	3	1	5	9	8	3	1	1	6	10	20	17	8	5	2	
K	12						1	1	3	3	3	10	11	20	24	21	2	1	
K	13			1	–	2	7	6	6	5	3	9	13	11	21	11	5		
K	28	1	4	13	11	18	11	11	5	1	5	3	6	4	4	1	2		

1933 continued : Tow-net hauls, means of surface, mid-water and bottom.

Cruise.	Station.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
K	12							1	1	3	–	4	11	15	25	15	14	9	1	1		
L	9				·7	·3	2	3	·3	1·3	2	8·7	13·7	23·7	22·7	13·3	6·3	2				
L	15			2·3	2·7	5·4	7·4	6·4	3·3	2	5	2·7	11·7	13·4	14·4	12	9	2		·3		
L	30				·7	3·3	7·3	6	4·7	2	2	5·3	13·4	15	17	12	6	3	1·3	–	·7	·3
L	35	·3	·7	1·4	10·8	13·6	25·1	15·9	9·8	4·1	3·1	1·4	2·7	3·1	3·0	2·4	1·7	·3	·3	·3		
Onaway 25	8						2	–	–	1	1	5	7	8	19	15	14	11	7	6	3	1
,,	9				·3	·3	·3	·7	·7	1·3	2	4·3	17·7	25·4	21·4	13·3	6	5·7	·3	·3		
,,	"Tea Kettle Hole"					1	–	1	–	2	6	6	17	27	19	13	7	1				

1934 : Hensen hauls.

Cruise.	Station.	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
C	19	1	2	4	14	29	15	12	11	10	1	–	–	–	1	–						
E	5			2	7	13	28	21	14	10	–	–	1	2	1	–	–	–	–	–	–	1
E	17								1	5	10	18	25	25	14	2						
G	5								2	3	10	17	24	17	12	10	3	2				
L	17						2	4	4	6	17	18	25	17	5	2						
M	3	3	15	10	7	5	2	1	2	10	11	16	12	5	1							
M	14					1	2	–	3	12	22	22	25	11	–	1	–	1				
M	21						3	–	4	6	33	19	26	8	–	–	1					
Onaway 35	6							1	3	16	25	22	23	8	2							

TABLE III.

Number of Cells of *Rhizosolenia alata* at Different Diameters in μ for Stations of Cruise M, 1934.

Diameter groups.	Free cells.																Auxospore forming cells.				Total.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	3–12	4–16	4–15	5–15	
Station 8		9	22	6	3									1			1	5	1	1	50
,, 17							1	11	23	43	9	7	3	3			–	–	–	–	100
, 15						1	0	8	13	47	17	9	2	3			–	–	–	–	100

TABLE IV.

(For explanation see text, p. 46)

	Northern neritic.				Temperate neritic.			Northern Oceanic.				
	Arctic Baltic.	Arctic.	Arctic Boreal.	Boreal.	N. Temperate.	Temperate.	S. Temperate.	Arctic.	Arctic Boreal.	Boreal.	Temperate oceanic.	Tropical and sub-tropical.
Melosira												
borreri . . .	–	–	–	–	–	25–60	–	–	–	–	–	–
hyperborea . .	–	14–30	–	–	–	–	–	–	–	–	–	–
Coscinodiscus												
excentricus* (50–90) .	–	–	–	–	–	–	–	–	–	–	–	–
lineatus . . .	–	–	–	50–60	–	–	–	–	–	–	–	–
leptopus . . .	–	–	–	–	–	?	–	–	–	–	–	–
nodulifer* . .	–	–	–	–	–	–	–	–	–	–	–	–
radiatus* (30–120) .	–	–	–	–	–	–	–	–	–	–	–	–
centralis . . .	–	–	–	–	–	–	–	–	–	–	120–300	–
sub-bulliens . .	–	–	–	–	–	–	–	–	–	65–150	–	–
commutatus† . .	–	–	–	–	–	–	–	–	–	–	–	–
concinnus . .	–	–	–	–	150–450	–	–	–	–	–	–	–
granii . . .	–	–	–	–	50–150	–	–	–	–	–	–	–
pavillardii . .	–	–	–	–	–	–	–	–	–	–	150–300	–
curvatulus . .	–	–	–	45–100	–	–	–	–	–	–	–	–
subtilis . . .	–	–	40–120	–	–	–	–	–	–	–	–	–
kutzingi . . .	–	50–63	–	–	–	–	–	–	–	–	–	–
joergensenii . .	–	50–80	–	–	–	–	–	–	–	–	–	–
stellaris . . .	–	–	–	–	–	–	–	–	–	–	75–175	–
Actinoptychus												
undulatus . .	–	–	–	–	–	40–140	–	–	–	–	–	–
splendens . .	–	–	–	–	–	–	70–180	–	–	–	–	–
Asteromphalus												
heptactis . .	–	–	–	–	–	–	–	–	–	–	50–100	–
hookeri . . .	–	–	–	–	–	–	–	–	–	–	25–50 (N. Temperate)	–
Actinocyclus												
ehrenbergi . .	–	–	–	–	–	55–156 (Cosmopolitan)	–	–	–	–	–	–
ralfsii . . .	–	–	–	–	–	50–200 (More southerly than *ehrenbergi*)	–	–	–	–	–	–
Thalassiosira												
nordenskiöldii . .	–	–	12–43	–	–	–	–	–	–	–	–	–
decipiens . .	–	–	–	–	12–40	–	–	–	–	–	–	–
gravida . . .	–	–	–	17–62	–	–	–	–	–	–	–	–
rotula . . .	–	–	–	–	–	35	–	–	–	–	–	–
fallax . . .	–	15	–	–	–	–	–	–		–	–	–
hyalina . . .	–	–	16–50	–	–	–	–	–	–	–	–	–
baltica† . . .	–	–	–	–	–	–	–	–	–	–	–	12–15
bioculata . .	–	–	–	30–60	–	–	–	–	–	–	–	–
condensata . .	–	–	–	–	–	17–30	–	–	–	–	–	–
subtilis . . .	–	–	–	–	–	–	–	–	–	–	15–32	–
Coscinoscira												
polychorda* (n 24–76)	–	–	–	–	–	–	–	–	–	–	–	–
œstrupi* (o 10–24) .	–	–	–	–	–	–	–	–	–	–	–	–
Lauderia												
borealis . . .	–	–	–	–	–	34–38	–	–	–	–	–	–
glacialis . . .	–	–	–	36–64	–	–	–		–	–	–	–
Schröderella												
delicatula . .	–	–	–	–	–	–	22–28	–	–	–	–	–
schröderi . .	–	–	–	–	13–40	–	–	–	–	–	–	–
Stephanopyxis												
turris . . .	–	–	–	–	–	–	35–65	–	–	–	–	–
palmeriana . .	–	–	–	–	–	–	–	–	–	–	–	80
Dactyliosolen												
antarcticus . .	–	–	–	–	–	–	–	–	–	–	38–68	–
mediterraneus . .	–	–	–	–	–	10–30	–	–	–	–		–
Leptocylindrus												
danicus . . .	–	–	–	–	6–11	–	–	–	–	–	–	–
minimus . . .	–	–	–	–	–	5	–	–	–	–	–	–

* Cosmopolitan species. † Brackish water forms.

TABLE IV. (cont.).

	Northern neritic.				Temperate neritic.			Northern Oceanic.				
	Arctic Baltic.	Arctic.	Arctic Boreal.	Boreal.	N. Temperate.	Temperate.	S. Temperate.	Arctic.	Arctic Boreal.	Boreal.	Temperate oceanic.	Tropical and subtropical.
Bacteriastrum												
delicatulum	–	–	–	–	–	–	–	–		–	12–40	–
hyalinum	–	–	–	–	–	–	20–55	–	–	–	–	–
elongatum	–	–	–	–	–	–	–	–	–	–	–	7–10
solitarium	–	–	–	–	–	–	38–48	–	–	–	–	–
Rhizosolenia												
alata f. genuina	–	–	–	–	–	–	–	–	–	–	7–15	–
alata f. gracillima	–	–	–	–	5–7	–	–	–	–	–	–	–
alata f. indica	–	–	–	–	–	–	–	–	–	–	–	40–70
obtusa	–	–	–	–	–	–	–	–	–	4–8	–	–
delicatula	–	–	–	–	–	–	14–20	–	–	–	–	–
færöense	–	–	–	–	25–70	–	–	–	–	–	–	–
fragillima	–	–	–	–	20	–	–	–	–	–	–	–
stolterfothii* (15–40)	–	–	–	–	–	–	–	–	–	–	–	–
cylindrus	–	–	–	–	–	–	–	–	–	–	–	26
robusta	–	–	–	–	–	–	–	–	–	–	–	160–170
shrubsolei* (10–40)	–	–	–	–	–	–	–	–	–	–	–	–
setigera	–	–	–	–	6–25	–	–	–	–	–	–	–
styliformis* (22–102)	–	–	–	–	–	–	–	–	–	–	–	–
calcar-avis	–	–	–	–	–	–	–	–	–	–	–	30–65
hebetata	–	–	–	–	–	–	–	–	4·5–12·5	–	–	–
acuminata	–	–	–	–	–	–	–	–	–	–	–	35–50
bergonii	–	–	–	–	–	–	–	–	–	–	–	100
castracanei	–	–	–	–	–	–	–	–	–	–	–	150
arafurensis	–	–	–	–	–	–	–	–	–	–	–	120
Chætoceros												
atlanticus	–	–	–	–	–	–	–	–	15–40	–	–	–
neapolitanus	–	–	–	–	–	–	–	–	–	–	13	–
janischianus	–	–	–	–	–	–	–	–	–	–	20–45	–
polygonus	–	–	–	–	–	–	–	–	–	–	–	12–15
densus	–	–	–	–	–	–	–	–	–	–	10–40	–
eibenii	–	–	–	–	–	–	30–45	–	–	–	–	–
borealis	–	–	–	–	–	–	–	–	14–46	–	–	–
glandazi	–	–	–	–	–	–	15–20	–	–	–	–	–
coarctatus	–	–	–	–	–	–	–	–	–	–	–	20
convolutus	–	–	–	–	–	–	–	–	11–30	–	–	–
convexicornis	–	–	–	–	–	–	–	–	–	–	–	17–30
concavicornis	–	–	–	–	–	–	–	–	12–34	–	–	–
danicus	–	–	–	–	–	8–20	–	–	–	–	–	–
tetrastichon	–	–	–	–	–	–	–	–	–	–	–	10
decipiens	–	–	–	–	–	–	–	–	12–78	–	–	–
mitra	–	–	20	–	–	–	–	–	–	–	–	20–50
lorenzianus	–	–	–	–	–	–	–	–	–	–	–	–
teres	–	–	–	18–48	–	–	–	–	–	–	–	–
lauderi	–	–	–	–	–	–	19	–	–	–	–	–
compressus	–	–	–	22	–	–	–	–	–	–	–	–
didymus	–	–	–	–	–	–	11–36	–	–	–	–	–
constrictus	–	–	–	14–35	–	–	–	–	–	–	–	–
affinis	–	–	–	–	–	–	9–22	–	–	–	–	–
laciniosus	–	–	–	7–42	–	–	–	–	–	–	–	–
brevis	–	–	–	–	–	20–21	–	–	–	–	–	–
diadema	–	–	11–46	–	–	–	–	–	–	–	–	–
coronatus	–	–	–	–	–	14–19	–	–	–	–	–	–
holsaticus	6–24	–	–	–	–	–	–	–	–	–	–	–
seiracanthus	–	–	–	–	–	12–24	–	–	–	–	–	–
difficilis	–	–	–	–	–	8–10	–	–	–	–	–	12–14
furca	–	–	–	–	–	–	–	–	–			–
diversus	–	–	–	–	–	10	–	–	–	–	–	–
similis	–	–	–	7–17	–	–	–	–	–	–	–	–
subtilis	5–15	–	–	–	–	–	–	–	–	–	–	–
wighami	7–15	–	–	–	–	–	–	–	–	–	–	–
perpusillus	–	–	–	4–5	–	–	–	–	–	–	–	–
filiformis	–	3	–	–	–	–	–	–	–	–	–	
exospermus	–	–	–	–	–	+? (Brackish water)		–	–	–	–	
karianus	–	–	–	–	–	–	–	15		–	–	
fragilis	–	–	–	–	–	–	–	8	–	–	–	–
crinitus	–	–	–	–	15–25	–	–	–	–	–	–	
pseudocrinitus	–	–	–	–	–	8–29	–	–	–	–	–	–
ingolfianus	–	–	–	–	–	9–18	–	–	–	–	–	–
curvisetus	–	–	–	–	–	–	10–29	–	–	–	–	–
debilis	–	–	–	–	12–29	–	–	–	–	–	–	–
pseudocurvisetus	–	–	–	–	–	–	26	–	–	–	28	–
adhærens	–	–	–	–	–	–	–	–	–	–	12–20	–
imbricatus	–	–	–	–	–	–	–	–	–	–		–

* Cosmopolitan species.

TABLE IV. (cont.).

	Northern neritic.				Temperate neritic.			Northern Oceanic.				
	Arctic Baltic.	Arctic.	Arctic Boreal.	Boreal.	N. Temperate.	Temperate.	S. Temperate.	Arctic.	Arctic Boreal.	Boreal.	Temperate oceanic.	Tropical and sub-tropical.
Chætoceros.—*contd.*												
externus	–	–	–	–	–	–	10–20	–	–	–	–	–
scolopendra	–	–	–	–	9–25	–	–	–	–	–	–	–
cinctus	–	–	–	–	–	–	5–15	–	–	–	–	–
furcellatus	–	8–20	–	–	–	–	–	–	–	–	–	–
tortissimus	–	–	–	–	–	11–16	–		–	–	–	–
socialis	–	–	4·5–15	–	–	–	–	–	–	–	–	–
radians	–	–	–	–	–	–	5–10	–	–	–	–	–
gracilis	–	–	–	6–10	–	–	–	–	–	–	–	–
septentrionalis	–	4–8	–	–	–	–	–	–	–	–	–	–
simplex	–	–	–	–	–	–	6–30	–	–	–	–	–
ceratosporus	–	–	–	–	–	10	–	–	–	–	–	–
Biddulphia												
biddulphiana†	–		–	–	–	–	60–90	–	–	–	–	–
aurita	–	–	–	–	30–80	–	–	–	–	–	–	–
mobiliensis	–	–	–	–	–	50–60	–	–	–	–	–	–
regia	–	–	–	–	–	–	60–180	–	–	–	–	–
sinensis		–	–	–	–	–	–	–	–	–	–	90
granulata	–	–	–	–	–	50–80	–	–	–	–	–	–
rhombus	–	–	–	–	–	50–180	–	–	–	–	–	–
obtusa	–	–	–	–	–	35	–	–	–	–	–	–
arctica†	–	–	–	100–300	–	–	–	–	–	–	–	–
favus	–	–	–	–	–	–	125	–	–	–	–	–
alternans	–	–	–	–	–	35–50	–	–	–	–	–	–
vesiculosa	–	–	–	–	–	50–140	–	–	–	–	–	–
Eucampia												
zoodiacus	–	–	–	–	–	–	25–73	–	–	–	–	–
greenlandica	–	? 13–20	–	–	–	–	–	–	–	–	–	–
Climacodium												
frauenfeldianum	–	–	–	–	–	–	–	–	–	–	–	100
biconcavum	–	–	–	–	–	–	–	–	–	–	–	35–65
Fragilaria												
islandica	–	13–49	–	–	–	–	–	–	–	–	–	–
oceanica	–	–	8–40	–	–	–	–	–	–	–	–	–
cylindrus	–	6–32	–	–	–	–	–	–	–	–	–	–
striatula	–	–	–	–	–	55	–	–	–	–	–	–
Asterionella												
japonica	–	–	–	–	–	–	50–85	–	–	–	–	–
kariana	–	–	–	37–68	–	–	–	–	–	–	–	–
notata	–	–	–	–	–	–	–	–	–	–	–	50–100
bleakeleyi	–	–	–	–	–	–	55	–	–	–	–	–
Thalassiothrix												
longissima‡	–	–	–	–	–	–	–	–	3000–4000	–	–	–
nitzschioides	–	–	–	–	10–80	–	–	–	–	–	–	–
frauenfeldii	–	–	–	–	–	–	–	–	–	–	100	–
Grammatophora												
serpentina	–	–	–	–	–	–	18–127	–	–	–	–	–
marina	–	–	–	–	–	–	10–104	–	–	–	–	–
Achnanthes												
tæniata	–	11–40	–	–	–	–	–	–	–	–	–	–
longipes	–	–	–	–	–	75	–	–	–	–	–	–
Navicula												
membranacea	–	–	–	–	–	–	50–90	–	–	–	–	–
septentrionalis	–	20–30	–	–	–	–	–	–	–	–	–	–
granii	–	50–57	–	–	–	–	–	–	–	–	–	–
pelagica	–	15	–	–	–	–	–	–	–	–	–	–
vanhöffeni	–	29–45	–	–	–	–	–	–	–	–	–	–
Nitzschia												
closterium* (20–90)	–	–	–	–	–	–	–	–	–	–	–	–
frigida	45–75	–	–	–	–	–	–	–	–	–	–	–
seriata	–	–	–	100	–	–	–	–	–	–	–	–
delicatissima	–	–	–	?	–	–	–	–	–	–	–	–

* Cosmopolitan species. † Bottom form or littoral not truly planktonic. ‡ Thread-like.

The Biology of *Purpura lapillus.* I. Shell Variation in Relation to Environment.

By

Hilary B. Moore, Ph.D.,

Marine Biological Laboratory, Plymouth.

With 11 Figures in the Text.

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INTRODUCTION.

Purpura lapillus Linn., more strictly known as *Nucella lapillus*, and frequently also as *Thais lapillus*, is a common carnivorous gastropod living between about half-tide level and extreme low water. While it does not usually extend below this level, occasional specimens are taken in some places down to a depth of several fathoms. It is not tolerant of strongly estuarine conditions, and it becomes less abundant on rocks where high wave-exposure is combined with absence of adequate sheltering crevices. It is also said to be absent from rocks which hang vertically over deep water (Agersborg, 1929).

Its geographic range on the east side of the Atlantic is from the west coast of Spain where it is locally plentiful, and Portugal where it is rare, throughout the coasts of the British Isles, France, Belgium, and Norway to the Murmansk coast and to one locality in Novaya Zemlaya, its extreme northern limit. These records have been assembled by Cooke (1915). It is absent from the Mediterranean, the Baltic and the White Sea. It is absent also from Spitzbergen and Jan Mayen Island, but occurs in the Faroe Islands and on the west and south coasts of Iceland. It is absent from the east coast of Greenland, and the records from the west coast seem doubtful. In North America it ranges from the southern coast of Newfoundland to about New York. Figure 1 shows this distribution, together with the positions of the summer and winter isotherms as given by Schott (1912). The northern limit of the species agrees fairly closely with the —1° C. winter isotherm, except on the American side, where it extends somewhat further north, and the limiting factor here seems to be the presence of regular winter ice on the shore. The southern limit lies closely along the 19° C. summer isotherm. These figures refer to oceanic water, and conditions would be more extreme on the shore. On the other hand, in winter at any rate, the Purpura tend to creep into sheltered crevices where their temperature probably does not fall much below that in the sea.

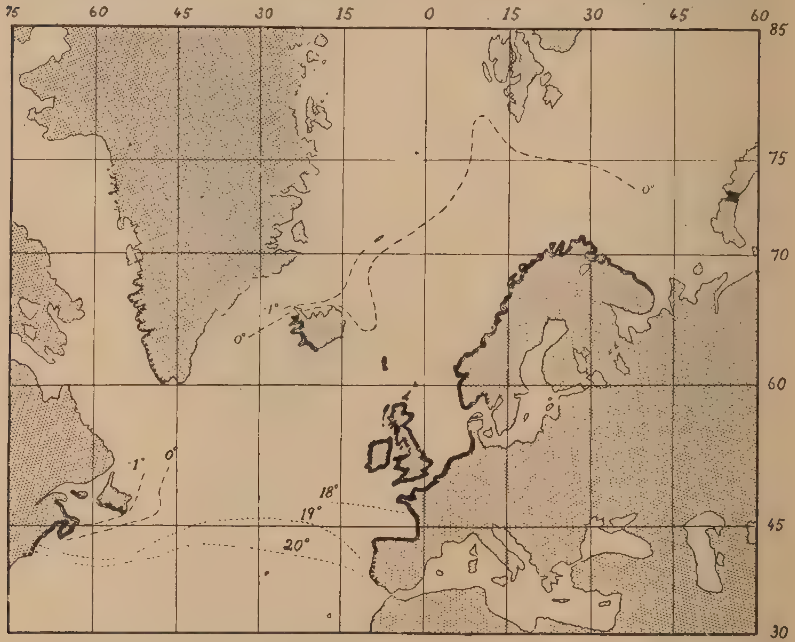


Fig. 1.—Geographical distribution of *Purpura lapillus*. The heavy lines show where it is abundant, and the dotted areas of coast where it is sporadic. The winter and summer isotherms are shown as discontinuous and dotted lines respectively.

Purpura lapillus, which is notoriously a very variable species, is for several reasons specially suitable for a study of variation in relation to environment. In the first place, the fact that it does not have a pelagic larva, and that the adults do not readily cross a barrier of either sand or deep water, renders each local community more or less self-contained, and the young of successive generations tend to disperse over the same area from which their parents were drawn. Variations would thus have a good opportunity of being perpetuated and becoming a characteristic of the community as a whole. In the second place it is very abundant, and can readily be collected in large numbers, and for this reason also it fits in with a survey in progress of the biology of the important littoral animals. Finally, as shown below, the obvious differences between populations from adjacent localities cover quite as wide a range as do the differences in populations from the extremes of the animal's geographical range.

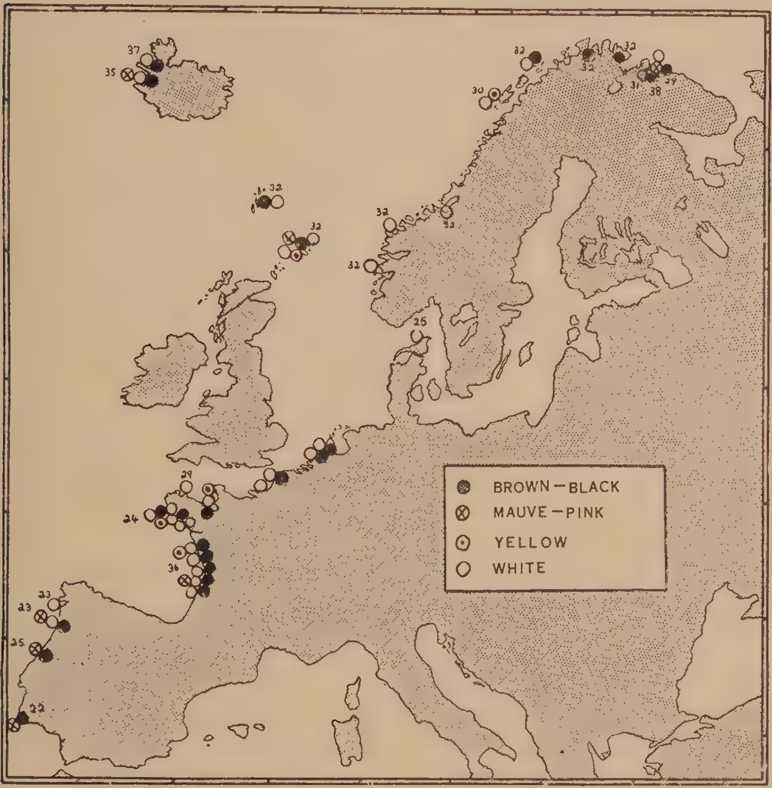
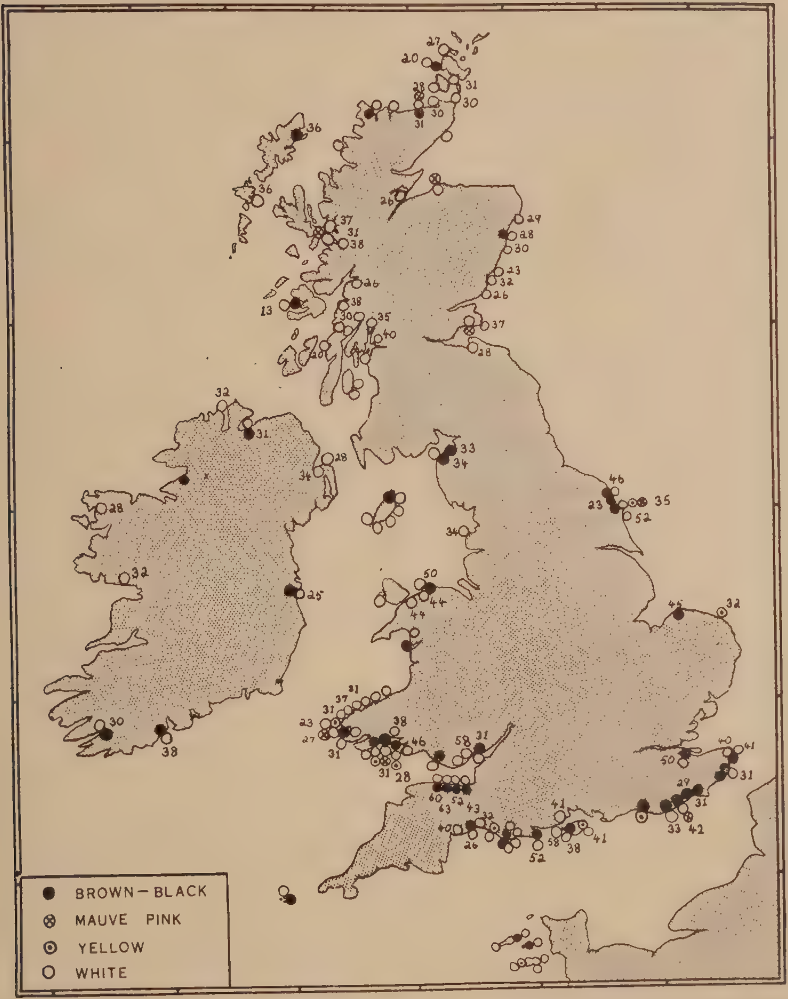


Fig. 2.—Distribution of localities from which coloured Purpura are recorded, and maximum heights (in mm.). Localities in the British Isles are shown in Fig. 3.

By the courtesy of the trustees of the British Museum it was possible to examine specimens of Purpura from a very large number of localities in the A. H. Cooke and other collections. Owing to the small size of the samples it was possible to make only a rough measure of a few characters, but this was sufficient to make clear one or two points. Although no actual measurements were made on shell angles, it was clear that there was no marked geographical trend of the apical angle θ (see p. 72). Colour, as is shown later (p. 79), is an index of the diet of the Purpura, and is therefore an important character. A note was taken of the presence or absence of the three principal colour types—brown-black, mauve-pink and yellow—in the sample from each locality. Since there is no evidence as to the degree of selection used in collecting these samples, deductions may only be drawn from a consideration of the general trend of the whole material. The colour distributions found in these collections, together with those from Mr. R. Winckworth's collections and that of the author, are shown in Figures 2, 3 and 4. In the latter, based on the author's own material, the actual percentages of brown-black specimens in the populations are shown. It will be seen that, although some localities, and even some limited areas such as the west of Scotland lochs, seem to contain only white shells, yet colour is generally distributed throughout their entire range from Portugal to Murmansk and Iceland, and to the American coasts also. Such local variation justifies the intensive study of a relatively small area of coast in an attempt to relate some of the observed variations to the environmental conditions supposed to produce them.

The size of the shells was the only character which showed any general geographical trend. The samples were of course inadequate for the determination of the mean size of the population, so in each case the height of the largest shell present was measured, and by grouping together all the results for a large area, significant results could thus be obtained. These maximum heights, wherever available, are shown in Figures 2 and 3. Three regions were taken, the first being the coast south of Cape Finisterre ; the mean value for the maximum height in this region was twenty-six millimetres, obtained from six localities. In the second region from Cape Finisterre north to latitude 60° N., which is just south of Bergen, the mean value was thirty-five millimetres, obtained from ninety-five localities ; while in the third region from 60° northwards the mean value was thirty-two millimetres from fourteen localities. Here therefore there seems to be a definite decrease in size towards the southern limit of the animal's distribution, and possibly a slight decrease also in the northern part of its range.

It seems to be a generally accepted theory that wave-exposure is the environmental factor responsible for most of the variations observed in Purpura. Cooke, for example (1895, p. 90), states : " Forms occurring in very exposed situations, e.g. Land's End, outer rocks of the Scilly Is., coasts of north Devon and Yorkshire, are stunted, with a short spire and relatively large mouth, the latter being developed in order to increase the power of adherence to the rock, and consequently of resistance to wave force. On the other hand shells occurring in sheltered situations, estuaries, narrow straits, or even on open coasts where there is plenty of shelter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30
38
● BROWN—BLACK
⊗ MAUVE PINK
⊙ YELLOW
○ WHITE

Fig. 3.—Distribution of localities from which coloured Purpura are recorded, and maximum heights (in mm.). Localities in the west of England are shown in Fig. 4.

from the waves, are comparatively of great size, with well-developed, sometimes produced spire and a mouth small in proportions to the area of shell surface." Wilkins (1934) confirms the belief that shells from a wave-exposed locality are stunted and have mouths large in proportion to their surface area. Agersborg also (1929, p. 47) records the tendency for the more acute shelled forms to occur in more sheltered, estuarine situations in Norway. On the other hand, Ökland (1933) records that the largest Purpura occur on the outer, more wave-exposed side of the island of Tromö, the salinity also being highest there.

With regard to colour, opinions differ, but Colton (1916) relates the abundance of coloured shells to the degree of wave action to which they are exposed, the colour being most abundant where there is most wave action. As will be shown later, none of these statements is a true representation of the facts.

MATERIAL AND METHODS.

Population samples were collected from seventy-six localities mostly on the coasts of Dorset, Devon and Cornwall. Over twenty-five thousand shells were collected, giving an average of 326 per sample, although, where Purpura was rare, the figures often fell far below this value (see Table I). The samples were made as representative as possible, their greatest error lying in the proportion of small shells which they contained. The latter tend to lie hidden in crevices, and hence to be inadequately represented in a sample, the extent of the error depending largely on the nature of the rock surface, and on the weather conditions prevailing at the time. Nearly all the samples were however collected in summer, when the young Purpura are most likely to be out on the open rocks, and only one characteristic (see p. 76) will be affected by this error. The material was preserved in formalin for later examination.

At the time of collection a note was made of the presence or absence of the two important barnacles on which the Purpura feed, *Balanus balanoides* and *Chthamalus stellatus*, and also of the degree of abundance of the mussel, *Mytilus edulis*. The latter was recorded under the following five categories :

—	Completely absent.
+	Either doubtfully present, or else absent in the immediate locality, but present in the neighbourhood.
++	Present in small numbers.
+++	Present in fairly large numbers.
++++	Present in very large numbers, and forming practically the whole diet of the Purpura.

Wave-exposure was measured by the method already applied in the study of barnacle distribution (Moore, 1935, p. 280). In this method the figure obtained represents the percentage of days throughout the year in which there is an onshore wind, and therefore sea, the aperture through which this can enter being taken at a distance of half a mile. While yielding adequate results for comparative studies, the method has not been used to compare localities outside the limited area of the west of England chosen for this study, nor can the method be used for a locality such as Tinside, Plymouth, which is sheltered from the open sea by a breakwater about two miles distant. The wind data used were ten-year means from the summaries published by the Meteorological Office for Portland Bill, Plymouth, Penzance and Newquay, each being applied to those localities nearest to it. On exposed headlands, and positions facing directly into the prevalent wind, very high values may be found, as for example at Pendeen Watch, Start Point and Hartland Point, each of which had a wave-exposure factor of seventy or over. In the first year's work, in which localities were chosen entirely at random, there was found to be a tendency for Mytilus to be most abundant on wave-exposed shores (apart from

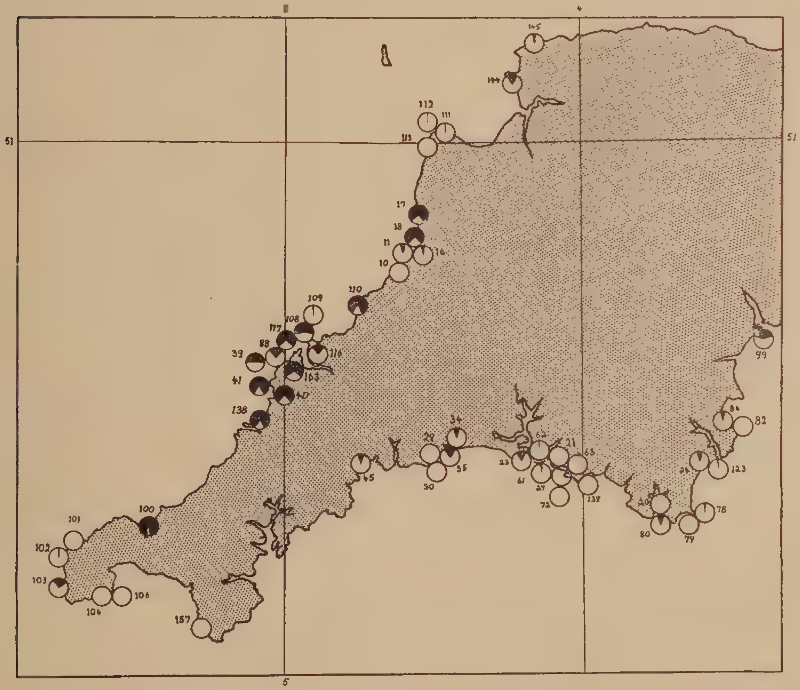
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Fig. 4.—The localities in the west of England used in the present work and their reference numbers (see Table I). The percentage of brown-black shells in each community is represented by the black sector in the circle.

muddy estuaries where Purpura does not penetrate), and this made it difficult to distinguish whether the Mytilus or the wave-exposure was influencing the several variable characters. In the second year therefore, in addition to increasing the number of localities, an attempt was made to include some representative of the two sets of conditions previously poorly represented, namely high wave-exposure together with absence of Mytilus, and shelter from waves with abundant Mytilus. The latter proved much the harder to find since in most such localities other conditions such as silt and low salinity tend to appear and to exclude Purpura. However, some examples such as Trebarwith Sands (110) were obtained.

Colour of the shell, which refers here to the outer surface only, was recorded under three headings, brown including black, mauve including pink, and yellow. Where two colour types were mixed in one shell it was recorded under both headings. A strong diffuse brown or black pigment has a tendency to mask a more delicate mauve tint, so that, where the two occur together, the figures for mauve may be somewhat too low. Boring filamentous algæ are responsible for a greenish brown coloration of the shells in some localities, *Gomontia polyrhiza* and *Plectonema terebrans* being the commonest species,* but such coloration is usually patchy, and readily distinguished from true pigmentation of the shell. In cases of severe infection the algal coloration may mask the true pigmentation of the shell and make it very difficult to recognise.

P. lapillus is a mollusc whose immature and mature shell types differ very considerably. The immature shell is growing fairly rapidly by increments to the free edge of the lip, which remains thin and sharp. At the onset of maturity growth of the lip ceases, and instead the region near the lip thickens, sometimes to as much as five millimetres, while the lip itself becomes rounded and a series of rounded teeth develop on its inner side which still further occlude the opening. In some communities a

* Identified by Mr. T. G. Tutin.

FIG. 5.

A. Mature, thick type shell, with marginal teeth and greatly occluded aperture.
B. Immature, thin-type shell, with thin-growing edge and very wide aperture.
C. Very small mature thick-type shell. Height, 13·0 mm. Nat. size.
D. Large thin-type (sub-littoral) Purpura. Height, 58·9 mm. Nat. size.
E. Var. *imbricata*.
F. Colour change from Mytilus type (dark) to Balanus type (light) under natural conditions.
G, H, I. Three views of a shell which shows the relation of colour to diet. G shows the original dark colour when the animal was feeding on Mytilus, and the sudden change to light (arrow) when transferred to Balanus. H shows the same shell rotated to the right. On the right is the light, Balanus produced area. At the arrows the diet was changed back to Mytilus, and to the left of this there is gradual recovery of pigmentation. I, rotated still further to the right, shows eventual complete recovery of pigmentation.

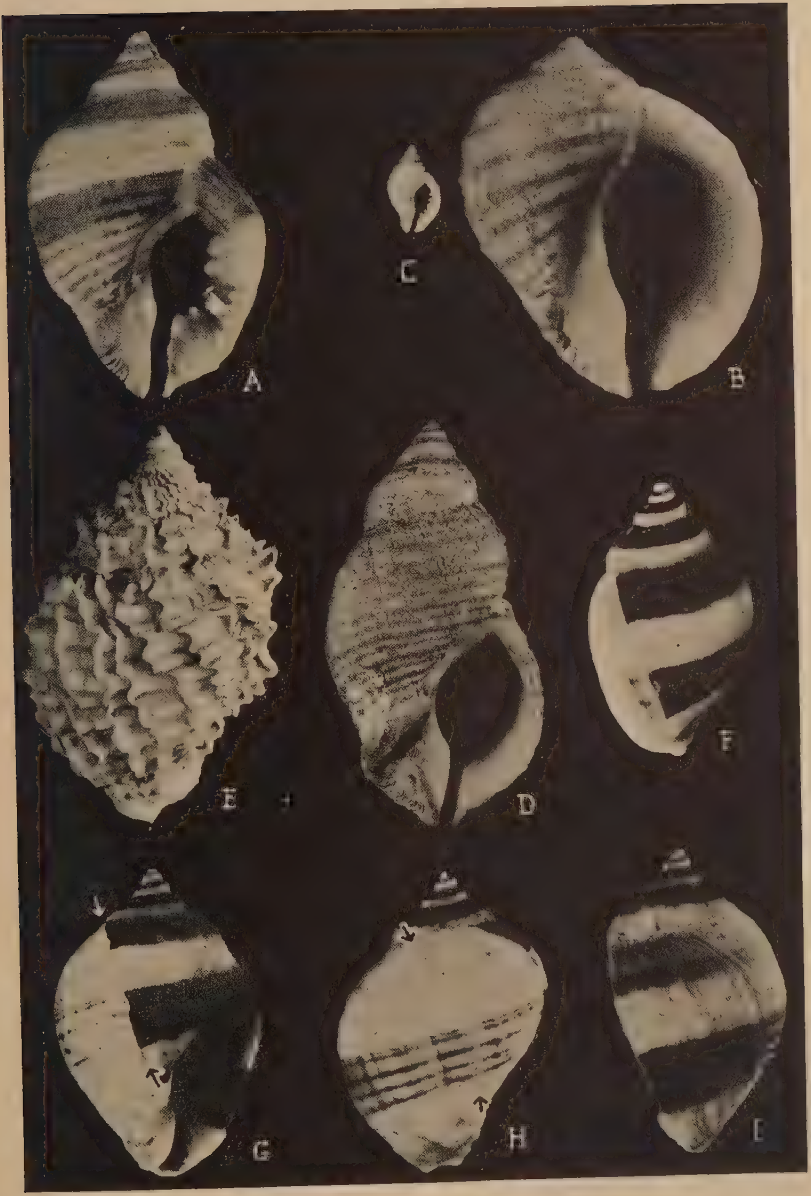

FIG. 5.

further tooth develops on the columellar margin of the aperture. Figures 5, A and B, show the great contrast between the relatively enormous area of aperture of an immature shell and the occluded opening of a mature one. In the two examples shown the area of the aperture of the immature shell (excluding the siphonal groove) represents 39% of the total projected area of the shell in the same plane, while that of the mature shell represents only 7% of that area, a difference of over five times. The fact that a Purpura can, on maturity, afford to reduce the size of its aperture to a fraction of its previous value surely indicates such a surplus of aperture size that the slight differences said to be observed between sheltered and wave-exposed communities could have no possible value in increased power of adherence to the rock. In any case the differences are shown later to have no connection with wave-exposure, but rather to be dependent on diet.

That increase of external size normally ceases completely when this lip thickening takes place has been demonstrated in numbers of individuals which were marked and released on the shore both at Plymouth and in the Isle of Man. When recaptured, even after a period of more than a year, these " thick " type shells showed no new increase whatever. Occasional specimens are taken in which the presence of a second set of teeth within the marginal ones indicates that the original stoppage of growth was followed by a second slight growing period, this in turn being replaced by a second period of thickening and growth stoppage, but such specimens are too rare to be a serious source of error. Owing to the great dissimilarity in the nature of the shells of the thin and thick types, it is necessary to treat them separately in certain of the measurements, as for example in estimating shell weight, and where this is done the two types are referred to as " thin " and " thick " types of shell respectively. Since growth ceases when the thickening occurs, the mean height of the " thick " type shells for any community is a measure of the mean size at which they matured (see p. 77), and is an important characteristic of the population. The figure varies greatly, " thick " type shells were recorded as small as 13 millimetres in height, and " thin " type as large as 63 millimetres (Fig. 5, C and D).

The size distribution of the entire population was estimated separately in millimetre groups for the thick and the thin type shells. The results were used in obtaining the mean thick type height, and also the percentage of thick type in the population. From the size-grouped material sets of twenty shells were taken, as far as possible at millimetre intervals, for shell weight and shape determinations. The height of each shell in the set was measured to the nearest 0·1 mm. They were then dried for forty-eight hours in a boiling-water oven, and weighed in group. As the tissue was left *in situ*, a correction had to be made to obtain the weight of the shell

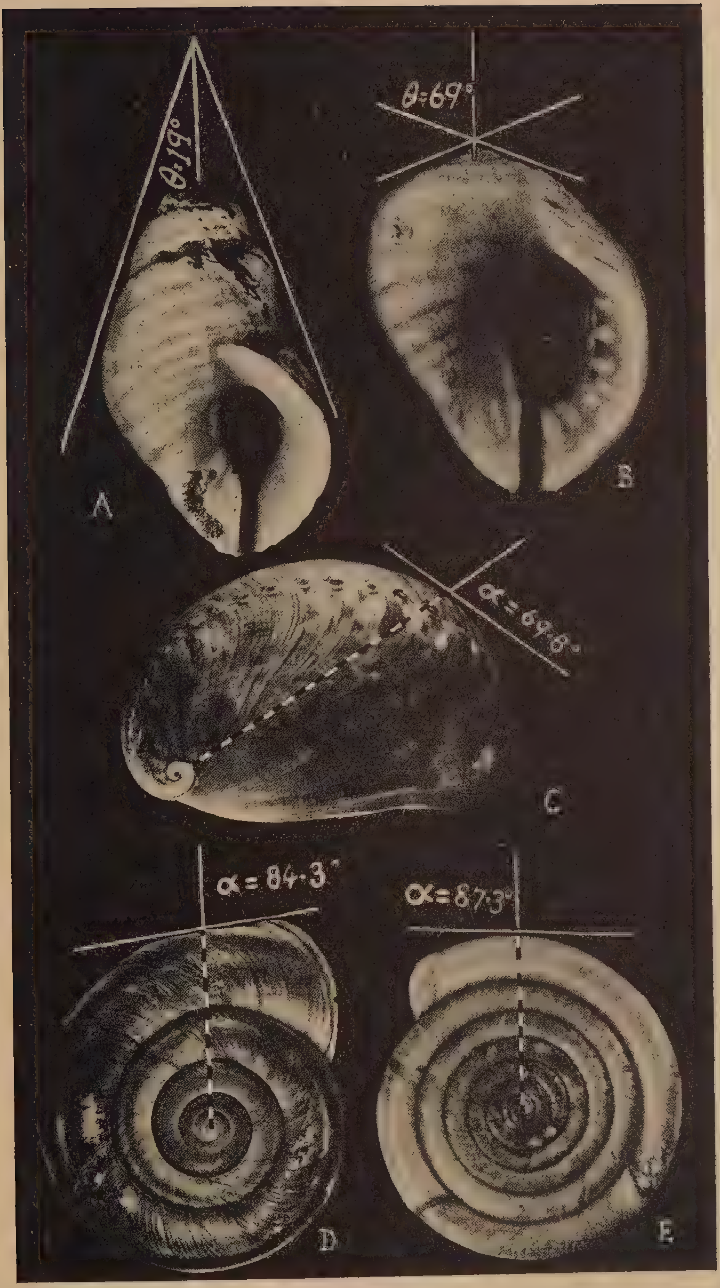

FIG. 6.

A, B. Extremes of variation in the apical angle θ in *P. lapillus*.
C, D, E. A series of shells, all viewed along their vertical axis (C and D from above, E from below), and illustrating the relation of the shape of the spiral to the spiral angle α. C, Haliotis. D, Helix. E, Planorbis.

alone, by multiplying by 0·956 for thin type shells, and by 0·960 for thick type. These factors were obtained from independent tissue-weight estimations on a number of samples. From the smoothed curves relating shell weight to height in each population, figures were obtained for the thick type shell weight at a height of 2·75 cm., a height at which the greatest number of populations could be included. Similar figures were obtained for both thick and thin types at a height of 2·3 cm., and the ratio of the latter two values was taken as a measure of the amount of thickening which had taken place at maturity, the figures so obtained ranging from 1·0, or no thickening, to 1·5, or an increase of 50% in weight.

As an expression of the shape of the shell, two characters have been taken, θ the half-apical angle, and α the angle of the logarithmic spiral of the shell. Both these values vary during the life of an individual, and the measurements taken refer to the last two whorls of the shell to be formed. The two angles can vary independently, although in Purpura a slight correlation was found between them due to their mutual correlation with a controlling factor, diet (p. 73). A low value of the apical angle θ corresponds to a tall spire such as that of Turritella. In an extreme case, *Terebra triseriata* Gray, θ is as low as 2·5°. In Purpura it usually lies between 35° and 40°, although extreme individuals vary much more widely. In a flattened shell like Planorbis, θ may be 90° or more. The effect of variation of α is less readily visualised. In Figure 6 are shown a series of shells illustrating variation of both θ and α. A low value of α represents an open spiral such as that of Haliotis (Fig. 6, C), a higher value of α represents a closer spiral like Planorbis (Fig. 6, E). Finally, on a very tall spire like *Terebra triseriata* it is possible to have a value of α as high as 89·2°, which, on a flatter shell would lead to impossibly tight packing of the whorls. Other things being equal, then, a decreased value of α means fewer whorls per unit height of shell. It must be realised that a very small change of α produces a very considerable change in the shape of the shell. Although there is a range of only about 3° between the extremes in all the populations of Purpura, this is as great as the difference in α between the Planorbis and the Helix shown in Figure 5.

θ was measured directly by means of a protractor somewhat similar to that illustrated by Thompson (1917, p. 529). α is not easy to measure directly except on a flat shell, and is more readily calculated from the formula :

$$\text{Tan } \alpha = \frac{2{\cdot}72 \text{ Sin } \theta}{\text{Log R}}$$

where θ is the observed half-apical angle, and R is the ratio of the diameters of two successive whorls (Thompson, 1917, p. 557). θ is introduced into the formula since the desired value of α is that for a plane spiral, and in the case of a shell it is projected on to a cone whose half-apical angle is θ. The fact that this method does not allow α to be calculated for the extreme lip of the shell introduces a slight lag in the observed values of α relative to the height of the shell (see p. 77). Since cessation of growth occurs when the shell commences to thicken, it does not matter whether the measurements of θ and α are made on thick or thin type shells, but in practice the latter were usually chosen as being cleaner and less corroded.

The individual measurements, about sixty thousand in all, are too numerous to publish, even as group means, but the characteristic values for each population, so far as they could be determined, are given in Table I. The resulting indications of relationships between the different characters are discussed in the following sections.

The Influence of Diet and Wave-exposure on the Shell.

Despite the assertions of various authors that wave-exposure influences both the shape and size of the shell, as well as its colour, detailed analyses of our results failed to show a single case of such a relation, with the possible exception of the abundance of yellow shells. As has already been stated, there is a tendency, in a random sample of localities, for those with the higher wave-exposure to have also a higher proportion of Mytilus replacing barnacles in the diet of the Purpura. But either an examination of the relative degrees of correlation of any character with abundance of Mytilus and with wave-exposure, or else a study of those localities where Mytilus is absent, show clearly that there is no direct correlation with wave-exposure. A detailed account of this is unnecessary, and it is sufficient to say that in every case such a correlation was tested for and found to be non-existent.

Since *Mytilus edulis* when abundant replaces either *Balanus balanoides* or *Chthamalus stellatus* in the Purpura's diet, the abundance of Mytilus may be taken as a rough measure of the proportion of mussels to barnacles in the diet.

The Relation of Shell-shape to Shell-size and to Diet.

The curves relating spiral angle α to height (Fig. 7)—height being used here as a measure of size—show a considerable variation, although a general pattern runs through most of them. Not all populations offer a sufficient range of size to yield a complete curve, but where this is obtained there is generally a fairly steady rise of α to a peak, followed, with increasing shell size by a drop in α, frequently to a level at which it thereafter remains constant (see Aberystwyth, Fig. 7). Where sufficiently small specimens were available, the rise to the peak was sometimes found to be preceded by a drop. Figure 7 shows four types of curves from different localities. The peak was found to be the most constant characteristic of these curves, so the value of α at the peak, and the shell height at which it occurred were taken as the two characteristics of the spiral angle.

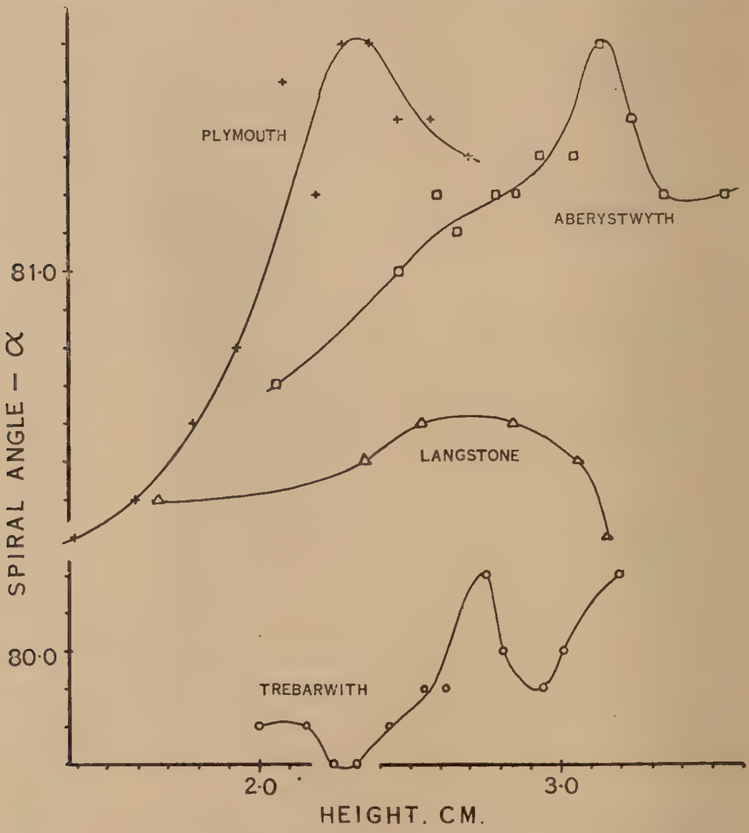

Fig. 7.—Curves relating spiral angle (α) to shell height for *P. lapillus* from four typical localities. For localities, see Table I.

That the value of α attained at the peak is not simply a function of the height at which the peak occurs is demonstrated by the absence of correlation when α is plotted against height at peak α.

The apical angle θ, when plotted against shell-height (Fig. 8), also tends to rise to a peak and then fall, but the peak is not always found, and here the drop in θ usually continues up to the largest sizes. Owing to the comparative steadiness of the drop it is possible to compare the value of

θ at a constant height (2·75 cm.) in different populations, a proceeding not possible with the more irregularly dropping α. A series of typical curves from four different localities is shown in Figure 8.

Taking these values of θ at H=2·75 cm. and peak α, and using all the populations for which such values are available, we find that both show

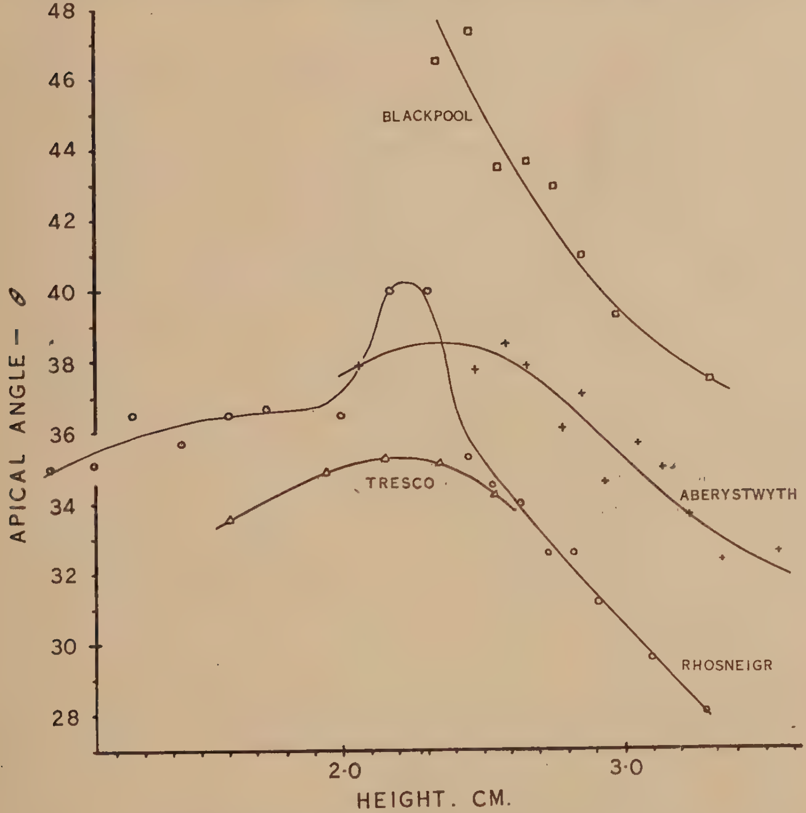

Fig. 8.—Curves relating apical angle (θ) to shell height for *P. lapillus* from four typical localities. For localities, see Table I.

a definite correlation with abundance of Mytilus but none with wave-exposure, nor is one found with wave-exposure when all Mytilus-fed communities are eliminated. The correlation* is good, $-0{\cdot}51 \pm 0{\cdot}12$ in the case of α and $+0{\cdot}51 \pm 0{\cdot}11$ in the case of θ. A slight secondary correlation of $-0{\cdot}27$ between the values for θ and α is due to their mutual dependence on Mytilus. Figure 9 is intended to show diagrammatically the relations between the various shell characters and the factors influencing them. Correlations are represented in it by whole lines if they are judged to be direct, and by dotted lines if they are secondary. Arrows indicate the directions in which the causes of the correlations are inferred to operate.

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* A correlation coefficient of 1·0 represents complete correlation, and a lesser value down to 0·0, a lower degree of correlation. Any value obtained can be regarded as significant if it exceeds twice its standard error. A positive sign indicates variation in the same direction, and a negative sign variation in opposite directions.

THE RELATION OF SHELL-WEIGHT TO SHELL-SHAPE.

It is obvious that, for a given height of shell, a bigger value of θ means a fatter, and therefore heavier shell. In the present work, correlation coefficients of $+0{\cdot}29$ and $+0{\cdot}32$ were found between the weights of the thin and thick types of shell respectively and θ. Similarly a change in α will affect the weight of the shell, a higher value corresponding to a shell with more whorls per unit length, and hence more connecting wall between the outside of the shell and the columella. The observed correlations here were $+0{\cdot}36$ and $+0{\cdot}45$ with the thin and the thick types respectively. Thus the diet influences the shape of the shell, and this in turn influences its weight; but while increase of Mytilus in the diet tends to increase θ it simultaneously decreases α and the two to some extent cancel out, so that the observed correlations of both θ and α with shell weight are in either case somewhat less than they would be were the other to remain constant. An additional result is that neither thick nor thin type shell weights show much correlation with the primary factor, abundance of Mytilus.

THE PROPORTION OF THICK AND THIN TYPE SHELLS IN THE POPULATION.

It has already been mentioned that in many localities there was a difficulty in collecting an adequate sample of the small Purpura (see p. 66). The proportion of thick type shells varied from 0 to 98%, a far greater range than could be accounted for by any error of collecting, and the percentage showed a good correlation ($-0{\cdot}42$) with abundance of Mytilus. The mean value for entirely barnacle-fed communities was 64% thick type, and that for Mytilus-fed (++++) only 28%. This character does not seem to be linked with any other, and is not likely to be understood until more is known of relative growth rates and mortalities under different conditions.

The Relation of Height at Cessation of Growth, Height at Peak α, and Degree of Thickening of the Mature Shell to Sexual Maturity, and the Relation of this to Abundance of Mytilus.

The height at which peak α occurs has a strong correlation (+0·76) with the mean thick type height, which is the mean height at which growth stops. Both have a weaker correlation with the abundance of Mytilus (+0·25 and +0·18, the latter being probably too low). Further, allowing for the lag in α already explained (p. 73), the height at which α changes proves, on the average, to be that at which growth ceases. Now if we consider the curve relating α to height for any given community, the individuals which have contributed that part of the α curve corresponding to a height greater than that at peak α are ones which have grown past the population's mean size for cessation of growth. And, although they have done this, they have responded at the size at which, were they average specimens, they should have stopped growing, by changing their spiral angle at that height. This leads to the supposition that the two characters are not directly correlated, but are mutually dependent on a third character, a likelihood which is borne out by their correlation coefficients (see above), and the most likely third character is sexual maturity. Assuming this, we can calculate approximately what the correlation coefficients should be between the various characters as shown in Figure 9. We find then a definite, but not very large correlation between sexual maturity and abundance of Mytilus, a very close correlation between height at cessation of growth and sexual maturity, and a close correlation also between the latter and height at peak α.

It was not possible to examine the sexual conditions of a large number of populations, but a single sample taken from Drake's Island, Plymouth, in July, 1935, was in complete agreement with the supposition that sexual maturity is the connecting factor governing cessation of growth. The sample was divided into three groups—thin shelled type, intermediate individuals whose shell was still growing but commencing to thicken, and non-growing, thick type shells. All animals were opened, and smears from their gonads examined. Ninety-seven thin type animals were examined, ranging up to 2·9 cm. high, and none of these showed ripe spermatozoa, or ripening or ripe ova. Eighty of the intermediate group were examined. Forty were males, and thirty-one of these contained active spermatozoa, those that did not being among the smallest specimens. Of the forty females, eleven contained maturing ova, the smallest again tending to show none. Finally, one hundred and ten thick type animals were examined, of which sixty-five were males. Sixty-three of these contained active spermatozoa, and the other two were heavily parasitised. Of the forty-five females, twenty-three contained ova in various stages of

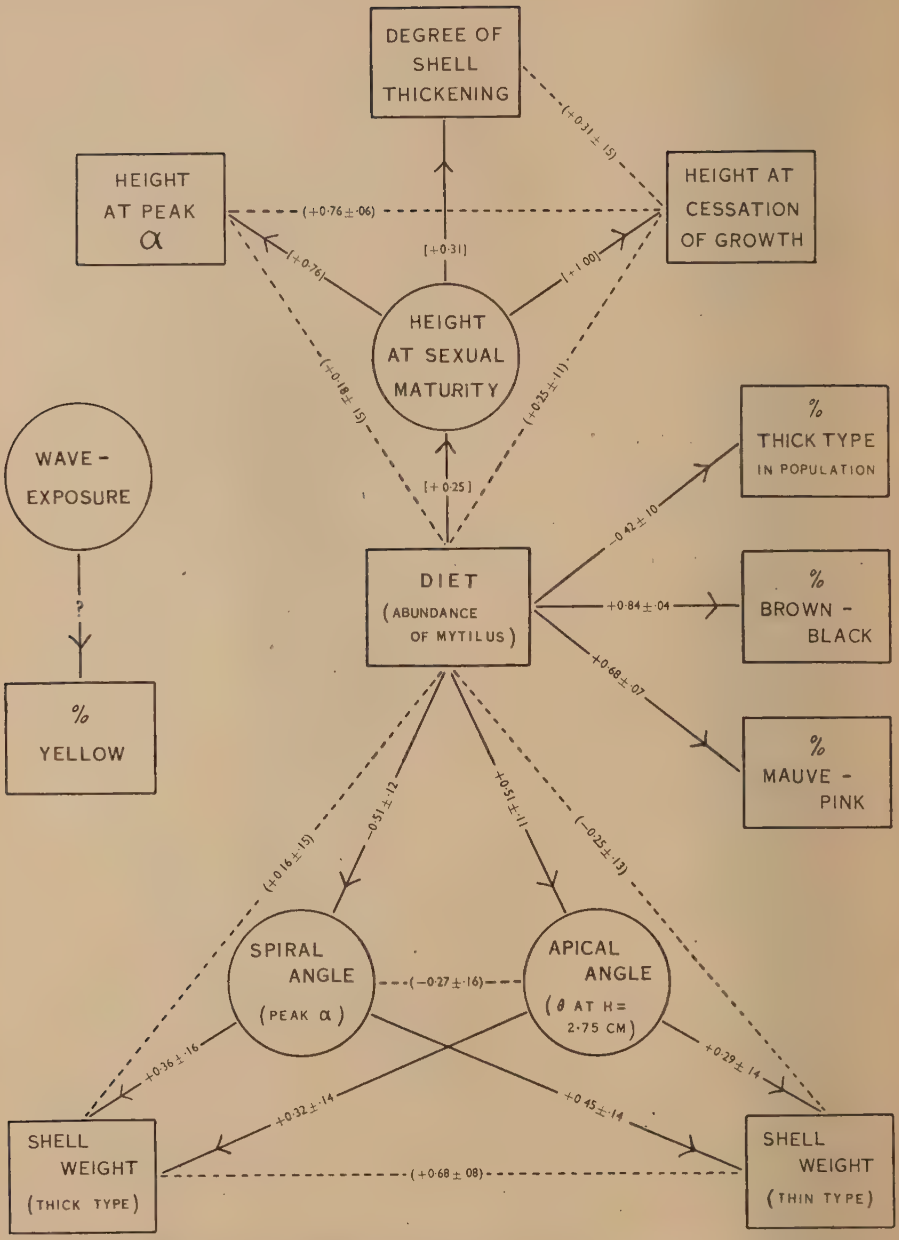
DEGREE OF SHELL THICKENING
HEIGHT AT PEAK α
HEIGHT AT CESSATION OF GROWTH
(+0·31 ± ·15)
(+0·76 ± ·06)
[+0·31]
(+0·76)
(+1·00)
HEIGHT AT SEXUAL MATURITY
(+0·18 ± ·15)
(+0·25 ± ·11)
[+0·25]
WAVE-EXPOSURE
?
% YELLOW
% THICK TYPE IN POPULATION
−0·42 ± ·10
DIET (ABUNDANCE OF MYTILUS)
+0·84 ± ·04
% BROWN-BLACK
+0·68 ± ·07
% MAUVE-PINK
(+0·16 ± ·15)
−0·51 ± ·12
+0·51 ± ·11
(−0·25 ± ·13)
SPIRAL ANGLE (PEAK α)
(−0·27 ± ·16)
APICAL ANGLE (θ AT H = 2·75 CM)
+0·36 ± ·16
+0·29 ± ·14
+0·32 ± ·14
+0·45 ± ·14
SHELL WEIGHT (THICK TYPE)
(+0·68 ± ·08)
SHELL WEIGHT (THIN TYPE)

Fig. 9.—Diagram of the relationships of the various characters and factors. Thick lines indicate direct, and dotted lines secondary correlations, and arrows their directions. The observed correlation coefficients are also shown, and their standard errors. Those in square brackets are calculated from observed secondary correlations (round brackets) and are only approximate. See p. 77.

development, the rest being probably spent, though this is not certain. These results show clearly, at any rate for this locality, the coincidence of sexual maturity and cessation of growth.

The degree of thickening of the shell at maturity is a third character whose close correlation with height at cessation of growth, and small correlation with abundance of Mytilus, suggests that the correlation works through the link of sexual maturity. The amount of thickening was not directly measured, but was estimated in terms of the ratio of the weights of the thick and thin types of shell at a height of 2·75 cm. The values range from no thickening at all and a ratio of 1·0 to a ratio of 1·5, or 50% increase in weight. The thickening is greatest at the lip, and as has been shown on page 70 may reduce the size of the aperture very greatly (Fig. 5, A and B). The value of this thickening of the shell is not evident. It may be a means of disposing of excess calcium carbonate no longer needed in enlarging the size of the shell. Flattely and Walton (1922, p. 112) have suggested that in certain species of Nassa the thickening of the lip may be a protection against the attack of hermit crabs. Another possibility is that the size of the aperture in the growing animal is quite unnecessarily large, so far as the protrusion of the foot and body are concerned. The outer boundary of the shell is fixed by the necessity of producing a definite shape of shell outline, and any thickening of the growing shell would result both in the production of an unduly heavy shell and in excessive closure of the cavity which is later to contain the visceral mass of the animal. When growth ceases, neither of these objections is operative, and the unnecessarily, and possibly dangerously large aperture can be reduced as much as is required. There is no apparent reason why animals reaching sexual maturity at a greater size should tend to require a greater degree of thickening of the mouths of their shells unless this is to counteract the more than usually large apertures resulting from the tendency for θ to be higher, and α lower than the average in such communities.

THE RELATION OF SHELL COLOUR TO DIET.

Colour variation in relation to environment is well known in many Mollusca. Wesenburg-Lund (1934, p. 184) gives an account of the blackening of the shells of certain Limnæas under the influence of parasitic Cercariæ. Pelseneer (1935, p. 380) gives a number of instances of molluscs whose shell colour, and even the colour of their eggs, is dependent on their diet. Colton (1916) states that in the Mount Desert region the abundance of coloured Purpura is greater with increasing wave-exposure, although showing a slight increase also in extreme shelter. He notes that there are more white shells in the Balanus zone than in the Mytilus zone, but appears to conclude that this is a case of adaptation, probably selective, to their environment. It has even been suggested (Cooke, 1895, p. 69), that the striped specimens of Purpura found in some localities are specially adapted for escaping notice on dark rocks veined with white quartz.

In the present work four colour types were distinguished. The first was white, sometimes masked by algal coloration (see p. 68). The second was brown which shades into black when more intense. This is the colour which shows the strongest tendency to longitudinal banding, although it may often be diffuse over the entire shell surface. The third colour type was mauve, grading through in very rare cases into pure pink. Although generally associated with brown, this colour is quite distinct from it. It is always diffuse, and I have never seen a specimen banded longitudinally with mauve on white. It may however be overlaid with bands of brown or black. When mauve is overlaid with diffuse brown or black, this may mask the mauve and result in some of the figures for this colour in Table I being too low.

The fourth colour type distinguished, yellow, sometimes shading into orange, and often extremely vivid, is quite distinct in its distribution from the other two. It is usually diffuse, although some specimens banded with yellow on white occur, and it may be found mixed with either of the other colours. The relation of yellow shells to environmental factors is very doubtful. It is definitely not correlated with abundance of Mytilus, but there seems to be some connexion, possibly secondary, with wave-exposure. All the populations of Purpura with a high percentage of yellow shells occur at wave-exposures lying between 20 and 60, yellow being practically absent in extreme shelter and extreme exposure (Fig. 10). The presence of yellow has also been found to be independent of the proportions of the two barnacles *Balanus balanoides* and *Chthamalus stellatus* in the diet, since on an almost pure Chthamalus diet the percentage of yellow has been found varying between 3% at Land's End and 32% at Tresco in the Scilly Is., while on a pure Balanus diet it varies from 0% at Port Erin, in the Isle of Man, to 96% at Redcliffe, Dorset.

The other two colour types, brown (Fig. 11) and mauve, are unquestionably dependent on the abundance of Mytilus in the diet. They show a close correlation, +0·84 and +0·68, with abundance of Mytilus, and none with wave-exposure except for the secondary one already explained (p. 73).

In order to test experimentally this dependence of colour on diet, a number of Purpura were kept on a controlled diet in tidal tanks in the laboratory. With yellow shells no conclusive results were obtained. White shells, from a Balanus-fed community, failed to show any pigmentation of their newly formed shell after a period of six months on a diet of Mytilus, but this may have been due to the too short duration of the experiment. It appears to require a long period of feeding on Mytilus before sufficient pigment is accumulated in the animal to appear in the new shell. This must be borne in mind in examining populations of Purpura on newly formed Mytilus beds. Coloured shells from a Mytilus-fed community were kept on diets of Chthamalus, Balanus and Mytilus respectively. Those fed on Mytilus showed no change in pigmentation in either the brown or the mauve types. In all the specimens fed on Chthamalus or Balanus, and in which there was sufficient growth of new shell, the amount of pigmentation in the new growth became less and less. The speed of this reduction varied considerably. In some, such as that shown in Figure 5, G, the change from black to white was immediate and almost complete, but in most it took place more gradually. Such specimens when finally replaced on a Mytilus diet eventually regained their original degree of pigmentation, as seen in the subsequent shell growth of the same specimen (Fig. 5, H and I). In this particular example, the pigmentation was regained very much more slowly than it was lost.

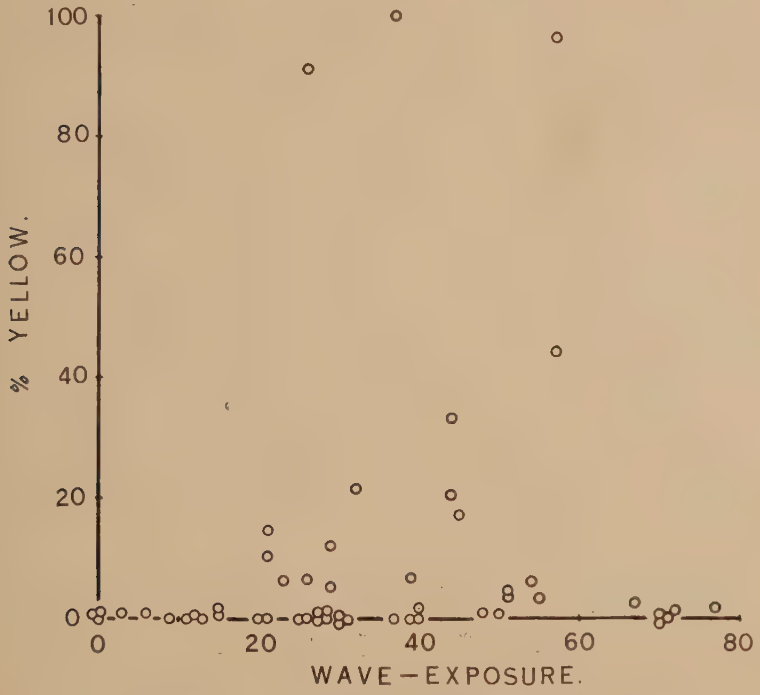

Fig. 10.—The relation of the abundance of yellow shells in the population to wave exposure.

A verification of the first part of the experiment was obtained under natural conditions by transplanting a number of strongly coloured, Mytilus-fed Purpura from north Cornwall to Drake's Island, Plymouth, where they had only Balanus to eat. In all those which survived, and showed a sufficient amount of new shell growth, there was a greater or lesser degree of paling of the original colour.

The effect of a change of diet, indicated by a transverse band of changed pigmentation cutting at right angles across the normal markings, is sometimes found in wild specimens. The change may be from coloured to white, as in the specimen shown in Figure 5, F, or *vice versa*. If we accept the presence of brown or mauve pigment in any part of the shell as evidence of a Mytilus diet at the time when that part of the shell was being produced, we find an interesting record in the shell of Purpura from localities where Mytilus is sparse and mostly confined to crevices. In such places we very often find that the large Purpura have white shells except for a small pigmented area at the apex. This suggests that when young they were feeding on Mytilus, and therefore living in the sheltered crevices, and that when they were older they came out on to the open

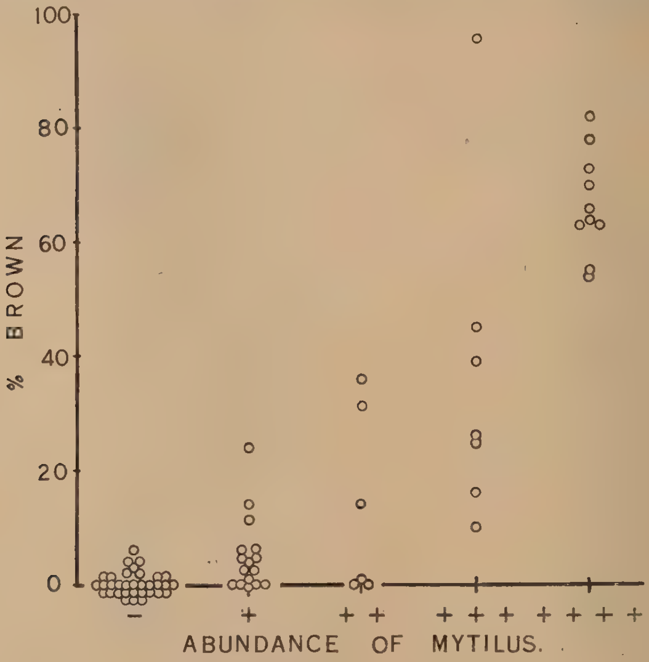

FIG. 11.—The relation of the abundance of brown-black shells in the population to the abundance of Mytilus in their diet.

rocks to feed on Balanus. This would be in agreement with our own observations on the habits of young Purpura, as well as with those of Colton (1916).

In Mytilus-fed communities, clusters of Purpura egg capsules are frequently found which are brownish or mauve instead of the yellow normally produced by Balanus-fed animals. The yolk in these capsules is strongly pigmented, and the young Purpura which hatch out from them are also strongly coloured. The pigment, however, affects only the first formed shell, and unless the young Purpura immediately commences to feed on Mytilus, the subsequently formed shell becomes white. There seems to be little doubt that these are the progeny of coloured parents, and that we have here a limited case of somatic inheritance.

The spiral pigment bands found on many Purpura shells are constant in position throughout the life of the animal, and vary only by intensification or dilution of their pigment. In the specimen shown in Figure 5, G, H and I, where the banding has been eliminated by a change in the diet of the animal, the pigment bands reappeared in the same position as before when the animal was replaced on a pigment-producing diet. That the banding is produced by localisation of the pigment in certain areas of the mantle edge can be seen on dissection of a banded specimen. The fact that some parts of the mantle edge may be loaded with pigment, while other parts are completely free from it, together with the fact that the width of the pigmented bands may vary so greatly in different individuals, suggests that in extreme cases the pigment-susceptible areas of the mantle edge may be narrowed to extinction, resulting in an animal which, though fed on a pigment-producing diet, would be unable to lay any of it down in its shell. This might account for the presence of a certain number of white-shelled individuals in a community apparently entirely fed on Mytilus.

Variation in Shells living below Low-water Mark.

Although normally living between tide marks, and probably in many cases deterred from colonising the sub-littoral zone by the heavy growth of algæ there, Purpura sometimes occurs several fathoms below low-water mark. There is very little information available on this subject, and I myself have never met with a locality where it happens, but Purpura are sometimes taken by fishermen in their inshore crab-pots, and a locality is known at Rhoscolyn where *P. lapillus* var. *imbricata* (Fig. 5, E) may be dredged from a submerged reef which is said to be covered with barnacles (*Balanus crenatus ?*). This var. *imbricata* is widely distributed, being recorded from places as far apart as Brittany, the Murmansk coast and America. In its most marked form it is a delicate shell which could not possibly survive undamaged if it were subjected to much wave action, and I have never found any but slightly imbricate shells between tide marks, and these among the younger specimens. On grounds such as Rhoscolyn the variety seems to be fairly common, although even there it is found living among large numbers of the typical form. It is possible that the imbrication is a phenomenon comparable with the "ledging" described in Patella (Moore, 1934) when kept permanently submerged. The Patella shell at first flattens, but later returns to its original shape, and it is possible that a rhythmical succession of such expansions and withdrawals, induced by the abnormal submerged conditions, might result in the formation of the lamellæ on the shell of var. *imbricata.* It is interesting to note that an allied species, *Thais* [=*Nucella*] *lamellosa* Gmel. from the American coasts, is normally imbricate in a very similar way, and Dall says (1916, p. 562) that it ". . . appears to frequent banks of rock and coarse gravel which are rarely uncovered by the tide, and yet are favourite haunts of barnacles, and of oysters, Anomias and other rough bivalves upon which the young Nucella feed."

Another character which seems to be associated with sub-littoral life is the excessive size of many of the Purpura. In the British Museum there are specimens up to sixty-three millimetres in height, whereas forty-five millimetres is a large size for the shore, and Mr. Tomlin has told me that many, if not most of these very large shells, which were taken at Minehead and Swanage, were obtained from crab-pots in depths of down to ten fathoms. Every shell of over fifty millimetres in length which I have been able to examine has been of the thin type, a fact which suggests that the giant size is due to the absence in these sub-littoral conditions of the factor which normally inhibits growth at maturity, and induces thickening of the shell edge. No soft parts were available for examination, but a parallel is suggested to the giant individuals produced as a result of parasitic castration in *Peringia* [=*Hydrobia*] *ulvæ* (Rothschild, 1936).

SUMMARY.

By examination of samples of *Purpura lapillus* from the whole of their European range, it appears that the species can exhibit quite as wide variation within a relatively small region such as that studied in the Dorset-Devon-Cornwall area, as it can over its whole geographic range. Population samples were taken from seventy-six localities, mostly in the south-west of England, and covering a wide range of environmental conditions, and the variations in these shells were studied in relation to two primary environmental factors, degree of exposure to wave-action and diet. Various authors have ascribed a strong influence on shell-shape and colour to the former, but the present examination shows that the only

character on which wave-exposure has any apparent effect is the abundance of yellow coloration in the shells. All other characters studied were found to be correlated either directly or indirectly with the nature of the diet, which varies from one of mussels (*Mytilus edulis*) to one of barnacles (*Balanus balanoides* or *Chthamalus stellatus*). Increase in Mytilus in the diet tends to produce a fatter shell with a more open spiral, and hence a wider aperture. Both these influence the weight of the shell, but as they act in opposite directions they tend to cancel out, and as a result there is little traceable relation between diet and shell weight.

Increase of Mytilus in the diet also decreased the proportion of mature (" thick " type) shells in the population, at the same time increasing the height at which sexual maturity sets in. Closely dependent on the onset of sexual maturity are the cessation of shell-growth with the concurrent thickening of the lip of the shell, as well as the degree of such thickening which takes place, and also the size at which the change in the spiral angle α occurs. Finally the two colour types brown-black and mauve-pink, whose pigments are derived directly from the Mytilus, are closely correlated in their abundance with the proportion of Mytilus in the diet, and may in fact be taken as an indicator of it. Two characteristics seem to be frequent in shells from a sub-littoral habitat, the variety *imbricata*, and a tendency to gigantism.

I wish to acknowledge my indebtedness to all those who have given assistance during this work and especially to Mr. G. M. Spooner for statistical treatment of the results : to the trustees of the British Museum for access to the Cooke collection, to Mr. R. Winckworth for access to his collection and for the loan of the shells illustrated in Fig. 6, C, D and E, to Dr. A. Gibson for very great assistance in collecting the north Cornish samples, to the staff of the Plymouth Laboratory, and to all the following who have kindly obtained samples for me : Mr. J. R. Bruce, Mr. R. Elmhirst, Dr. E. Fischer-Piette, Mr. W. Fowler, Mr. J. H. Fraser, Dr. F. P. Koumans, Mr. W. J. Rees, Mrs. R. S. Sturdy and Dr. E. Wordley.

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TABLE I

Observed Characteristics of the Populations of *Purpura lapillus* Examined, and of the Localities. All heights in cm.; weights in gm. Figures in brackets are approximate only.

For map of localities see Fig. 4. N.D.=North Devon. S.D.=South Devon. N.C.—North Cornwall. S.C.=South Cornwall.

Locality.	Reference number.	Wave-exposure factor.	Abundance of Mytilus.	Presence of Chthamalus.	Presence of *B. balanoides*.	Number of specimens.	Maximum height.	Mean height of thick type.	Percentage thick type in population.	Percentage of brown-black.	Percentage of mauve-pink.	Percentage of yellow.	Thick-type weight (height=2·75 cm.)	Thick-type weight (height—2·3 cm.).	Thin-type weight (height= 2·3 cm.).	Thick-type weight. / Thin-type weight.	Apical angle θ (height=2·75 cm.).	Spiral angle α. Peak value.	Height at peak value of α.
Crackington Haven (N.C.)	10	15	++	+	+	350	3·2	2·25	70·5	0·3	0	1·2	4·0	2·5	2·2	1·14	38·1	81·2	(2·4)
Millook Haven (N.C.)	11	37	+	+	+	42	2·5	2·03	81·0	14·2	0	0	—	—	—	—	—	—	—
Wanson Mouth (N.C.)	16	55	+	+	+	171	2·9	1·99	89·7	5·3	0	3·2	4·3	2·8	—	—	39·0	81·6	2·2
Salthouse (N.C.)	17	54	++++	+	+	244	3·3	2·74	92·6	62·7	15·2	5·7	4·1	2·4	2·1	1·14	40·8	—	—
Duckpool (N.C.)	18	45	++++	+	+	111	3·0	2·94	3·6	66·0	39·3	17·0	—	—	1·5	—	40·3	(80·3)	—
Church Reef, Wembury (S.D.)	19	29	++	+	+	133	3·0	2·42	48·2	0·6	4·5	12·0	3·4	2·4	2·0	1·20	36·4	81·4	2·3
Biddlehead, Salcombe (S.D.)	20	6	—	+	+	327	3·6	2·87	81·8	0	0·3	0·6	4·7	3·2	2·4	1·33	40·8	81·8	2·9
Rum Bay (S.D.)	21	32	+	+	+	200	3·4	2·72	65·5	0·5	0	21·2	3·2	2·2	1·8	1·22	34·1	81·4	2·5
Pier Cellers, Cawsand (S.C.)	23	44	+	+	+	242	3·3	2·64	59·2	24·2	0	20·2	4·5	3·2	2·8	1·14	37·7	81·8	2·7
Polperro, Loc. D. (S.C.)	29	3	—	+	+	156	2·9	2·29	71·8	0	0	0·6	3·9	2·5	2·4	1·04	(37·0)	81·7	2·1
Polperro, Loc. E. (S.C.)	30	30	—	+	+	55	2·4	1·99	89·2	0	0	0	—	—	—	—	—	—	—
Limmicks, Looe (S.C.)	34	29	+++	+	+	189	3·2	2·66	65·7	10·0	3·0	5·0	4·2	3·1	2·4	1·29	37·8	81·7	2·5
Hannafore Point (S.C.)	35	48	++	+	+	300	3·2	2·45	58·4	31·1	0	0·7	2·7	1·8	1·6	1·12	32·5	81·0	2·3
Treyarnon Beach (N.C.)	39	51	++++	+	+	164	3·6	2·66	65·8	55·4	34·3	4·8	4·1	—	2·3	—	42·8	81·1	2·6
Mawgan Porth (N.C.)	40	50	++++	+	+	188	3·5	2·81	8·9	70·2	37·4	0·5	3·7	—	1·7	—	41·0	80·2	2·7
Bedruthan Steps (N.C.)	41	51	++++	+	+	241	3·1	2·46	6·9	72·6	28·6	3·2	2·8	—	1·6	—	41·4	(80·1)	—
Charlestown (S.C.)	45	28	+	+	+	279	3·0	2·48	70·9	11·3	0	1·4	4·2	2·7	2·3	1·17	39·6	82·9	2·1
Plymouth Breakwater (outside) (S.D.)	61	21	+	+	+	347	2·9	2·43	65·4	4·1	0	10·2	4·1	2·4	2·2	1·09	38·3	81·6	2·3
Plymouth Breakwater (inside) (S.D.)	62	—	+	+	+	307	3·1	2·34	72·9	1·9	0·3	14·1	4·1	2·5	2·1	1·19	35·5	82·2	2·3
Misery Point, Yealm (S.D.)	63	0	—	+	+	662	3·2	2·55	60·5	0·3	0	1·4	3·5	2·3	2·1	1·09	37·1	81·6	2·1

TABLE I—*contd.*

Locality.	Reference number.	Wave-exposure factor.	Abundance of Mytilus.	Presence of Chthamalus.	Presence of *B. balanoides*.	Number of specimens.	Maximum height.	Mean height of thick type.	Percentage thick type in population.	Percentage of brown-black.	Percentage of mauve-pink.	Percentage of yellow.	Thick-type weight (height 2·75 cm.)	Thick-type weight (height=2·3 cm.).	Thin-type weight (height=2·3 cm.).	Thick-type weight / Thin-type weight.	Apical angle θ (height=2·75 cm.).	Spiral angle α. Peak value.	Height at peak value of α.
Drake's Is., N. side (S.D.) .	67	0	++	+	+	808	3·7	2·95	54·7	—	—	—	4·5	3·0	2·4	1·25	—	—	—
St. Servan, Loc. A. (France) .	70a	—	.	.	.	211	2·6	2·16	60·2	23·7	5·2	0	—	2·0	1·7	1·18	—	81·3	2·2
St. Servan, Loc. B (France) .	70b	—	++++*	.	.	199	2·7	2·15	88·5	3·0	1·0	1·0	—	1·9	—	—	—	81·5	2·3
St. Servan, Loc. C (France) .	70c	—	+++*	.	.	90	2·8	2·27	86·7	5·6	5·6	2·2	—	1·9	—	—	—	80·9	2·3
Gara Point (S.D.) . . .	72	15	—	+	+	178	2·7	2·20	58·5	0	0	1·7	—	2·4	2·2	1·09	—	81·1	2·2
Start Point (S.D.) . .	78	70	—	+	+	52	3·2	2·69	48·1	5·8	0	0	—	—	—	—	—	—	—
Lannacombe Beach (S.D.) .	79	21	—	+	+	373	3·5	2·77	89·1	0	0	0	4·0	2·5	2·4	1·04	37·5	81·2	2·6
Black Cove (S.D.) . . .	80	11	+++	+	+	30	2·5	2·28	36·7	16·1	12·9	0	—	—	—	—	—	—	—
Mudstone Sands (S.D.) . .	82	13	—	+	+	516	3·4	2·81	79·7	0·2	0	0	3·0	2·9	2·5	1·16	37·6	81·2	2·7
Saltern Cove (S.D.) . .	84	28	+	+	+	647	3·1	2·32	74·9	6·2	0	0	3·5	2·5	2·2	1·14	35·5	81·5	2·1
Trevose Head (N.C.) . . .	88	77	+++	+	(+)	130	3·2	(1·99)	11·5	39·2	44·6	1·5	—	—	—	—	—	—	—
Penrhyn Bay (Wales) . .	94	—	+	—	+	899	3·7	2·48	57·8	0	0	0	3·4	2·2	1·9	1·16	32·4	—	—
Rhosneigr (Anglesey) . .	95	—	—	—	+	734	3·4	2·87	44·4	0·5	0	18·8	3·5	2·2	1·9	1·16	32·8	81·9	2·3
Aberdeen	97	—	—	—	+	266	3·1	2·47	85·3	0	0	0	4·5	2·9	—	—	33·8	—	—
Langstone Rock, Dawlish (S.D.)	99	23	+++	+	(—)	148	3·7	2·80	23·7	44·9	47·6	6·1	—	—	2·4	—	40·1	80·6	2·7
St. Ives (N.C.) . . .	100	(16)	+++	+	+	348	3·5	2·77	59·8	95·7	1·4	0	3·4	2·3	1·8	1·28	36·9	80·8	2·8
Pendeen Watch (N.C.) . .	101	70	—	+	(—)	635	2·8	2·10	98·5	0·5	0	0	—	3·0	—	—	—	82·1	2·2
Cape Cornwall (N.C.) . :	102	72	+	+	+	409	2·9	2·19	68·4	2·7	0	1·2	3·7	2·7	2·4	1·12	—	—	—
Land's End (N.C.) . .	103	67	+++	+	+	115	2·6	2·16	46·9	25·5	8·2	2·7	—	2·6	—	—	—	80·8	2·2
Porthcurno (S.C.) . . .	104	9	—	+	—	822	2·6	1·89	88·6	0	0	0	—	2·6	—	—	—	—	—
Ushant (France) . . .	105	—	+	.	.	176	3·1	2·53	48·8	1·7	0	0	4·3	2·8	2·2	1·27	37·2	82·3	2·7
Treryn Dinas (S.C.) . .	106	40	—	+	+	248	2·8	2·33	82·7	0·4	0	1·6	3·8	2·5	2·1	1·19	37·2	82·2	2·5
Hayle Bay (N.C.) . . .	108	26	++++	(+)	+	577	3·5	2·63	1·2	54·0	40·1	6·6	—	—	1·4	—	39·3	—	—
Portquin (N.C.) . . .	109	0	+	(+)	+	557	3·3	2·38	59·4	1·4	0	0·7	4·1	2·6	2·3	1·13	37·2	—	—
Trebarwith Sands (N.C.) .	110	12	++++	+	+	619	3·5	2·70	4·0	78·0	63·9	0·5	3·7	—	1·7	—	43·2	80·2	2·7
Shipload Bay (N.D.) . .	111	30	—	+	+	687	3·0	2·18	83·8	1·7	0·1	0	4·5	2·8	2·4	1·17	40·3	81·5	2·1
Hartland Point (N.D.) . .	112	71	—	+	+	411	2·3	1·90	79·3	3·2	6·1	0	—	2·6	—	—	—	81·9	2·0

Hartland Quay (N.D.)	113	39	—	+	+	766	2·4	1·88	91·0	0·8	0·8	0	-	2·6	-	—	—	—	—
Red Rocks Cove (Berwick)	115	—	++	·	·	596	3·0	2·43	65·8	0	0	0	3·8	2·2	2·0	1·10	37·6	—	—
The Greenaway (N.C.)	116	21	++	(+)	(+)	72	3·5	2·96	34·8	35·8	18·6	14·3	—	—	3·0	—	—	—	—
Harlyn Bay (N.C.)	117	28	++++	(−)	+	442	3·6	2·90	30·8	63·7	13·0	1·1	3·6	—	2·0	—	41·6	80·4	2·8
Blackpool (S.D.)	123	26	—	+	+	373	3·8	2·62	96·1	1·3	0	0	—	—	—	—	41·8	81·4	2·8
Mathew's Point (S.D.)	124	31	++	+	+	445	3·5	2·13	47·8	13·7	3·6	0	—	2·8	2·8	1·00	43·5	—	—
Tresco (Scilly Is.)	127	—	—	+	—	117	2·8	2·43	14·5	0	0	31·7	-	—	1·7	—	—	80·5	2·1
Carsaig, west (Argyll)	129	—	—	—	+	234	2·9	2·46	78·2	0	0	0	4·5	2·8	2·6	1·08	40·0	80·7	2·3
Carsaig, east (Argyll)	130	—	—	(−)	+	412	3·2	2·68	81·3	0	0	0	4·1	—	—	—	34·4	—	—
Domburg (Holland)	132	—	(++++)	·	·	52	3·1	—	0	50·0	0	10·4	—	—	—	—	—	—	—
Balta Sound, Unst. (Shetland Is.)	135	0	—	·	+	161	3·7	2·92	54·0	4·3	0	0	4·4	—	—	—	35·9	81·7	2·8
Fistral Bay (N.C.)	138	28	++++	+	+	372	3·6	2·80	45·4	82·1	(1·6)†	0·5	4·2	2·5	2·3	1·09	43·0	—	—
Stoke Beach (S.D.)	139	20	+	+	+	805	2·7	2·18	68·3	0	0	0	—	2·6	2·4	1·08	—	81·6	2·2
Lyme Regis (Dorset)	141	37	—	+	+	20	2·6	2·28	35·0	0	0	100·0	—	—	—	—	—	—	—
Port Erin (Isle of Man)	143	—	—	—	+	691	3·7	2·79	28·7	0·1	0·1	7·8	3·7	2·7	1·8	1·50	—	—	—
Saunton Down (N.D.)	144	57	+++	+	+	363	3·6	2·66	35·0	25·6	3·0	44·1	4·0	2·2	1·6	1·37	38·2	81·0	2·7
Lee Bay (N.D.)	145	40	—	+	+	336	3·2	2·38	93·5	4·5	0·3	0	3·9	2·7	2·2	1·23	34·9	81·4	2·2
Redcliff (Dorset)	154 160	57	+	(−)	+	726	3·6	2·82	46·0	6·2	0	96·4	3·7	2·3	2·0	1·15	34·7	—	—
Aberystwyth (Wales)	155	—	—	—	+	515	3·7	2·88	91·7	0	0	0	4·3	2·6	2·3	1·13	37·1	81·5	3·2
Hook of Holland	156	—	(++++)	·	·	95	3·1	2·72	15·8	44·2	5·3	0	3·3	—	1·5	—	—	80·3	2·5
Porth Mellin (S.C.)	157	25	—	+	(+)	13	3·5	2·10	38·4	0	0	0	—	—	—	—	—	—	—
Whitenothe (Dorset)	158	44	—	(−)	+	106	3·0	2·47	17·9	0	0	33·0	—	—	1·9	—	—	—	—
Nothe (Dorset)	158a 162	26	—	(−)	+	239	3·3	2·87	28·9	0	0	91·2	3·6	—	1·8	—	36·0	—	—
Bincleaves (Dorset)	161	(0)	—	—	(+)	59	3·7	3·00	42·4	0	0	3·4	—	—	—	—	—	—	—
Kames Bay, Cumbrae (Bute)	M.1	—	(+)	(+)	+	456	3·2	2·43	11·6	0	0	0	—	2·2	2·0	1·10	34·2	80·9	2·0
Farland Point, Cumbrae (Bute)	M.2	—	+	(+)	+	328	3·6	2·62	39·5	0	0	0	2·9	1·8	1·7	1·06	34·7	—	—
Whiting Bay, Arran (Bute)	M.5	—	—	(+)	+	167	3·4	2·84	31·1	0	0	0	3·2	—	1·8	—	33·9	81·3	2·9
Largy Beg, Arran (Bute)	M.6	—	—	(+)	+	254	3·4	2·76	26·7	0	0	0	3·5	—	1·9	—	36·3	—	—
Fairlie Pier (Ayr)	M.7	—	(+)	—	+	216	4·2	2·92	35·7	5·0	0	0	—	—	—	—	36·3	81·3	2·7

* Mytilus colonies only recently established.

† Mauve much masked by brown, giving too low a figure.

The Occurrence of *Diadumene cincta* T. A. Stephenson in the River Roach, Essex.

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Several small anemones resembling *Metridium dianthus* were collected from the River Roach and sent to me in the summer of 1934. A careful examination proved them to be *Diadumene cincta* which was first recorded from Plymouth. T. A. Stephenson (**1**, 1925, p. 880) described both an orange and a fawn variety of this species, the former from the Breakwater and the latter from the Pier, Plymouth. The Roach anemone agrees with the Plymouth one in all its more important habits and its external and internal characters. It would appear that the specimens of *D. cincta* from the New England Creek, Essex, recorded by T. A. Stephenson (**2**, 1935) since this account was first written, may have been derived from this river.

The anemones were dredged in abundance from the River Roach attached to living and dead shells of Ostrea and Mytilus and to Alcyonidium and Halichondria. All (about thirty) which I have seen were small, the diameter of the base averaging 0·6 cm. and the disc 1·5 cm. They were orange, but some were pale while others were more deeply coloured. No fawn ones have as yet been found in this locality.

The scapus wall is thin, translucent with a bluish caste and with the mesenterial insertions showing through. The cinclides are evident as distinct dull purple-grey spots, each with a central depression clearly visible under a hand lens. The tentacles are the same colour but paler than the scapus. They are usually uniformly coloured but in some specimens there are two faint bluish lines running along their upper surface and, in one individual, there was a pair of short dashes at their bases instead of these lines. The lip lobes are ribbed, deep red-orange and sometimes with an irregular white powdering at their bases. (In the fawn but not in the orange variety from Plymouth there is an opaque cream bar at the bases of the outer tentacles.)

The anatomy of an Essex specimen which was sectioned agrees in all its main features with that described by E. M. Stephenson (**3**, 1925, p. 897) for *D. cincta* except that the cinclides are mainly very definite, imperforate, endodermal evaginations instead of imperforate, ectodermal invaginations.

Both spirulæ and penicilli are very abundant in the acontia. Their sizes correspond with those given by T. A. Stephenson (**4**, 1929, p. 173) and my own records for *D. cincta* from Plymouth (see Table I). The penicilli resemble in form those from the acontia of *Metridium dianthus* (**5**, 1934, p. 910, Fig. 2), except that they all have a distinct long terminal thread and their capsules are much wider. The spirulæ are different in form and very much smaller than those of *M. dianthus* (**4**, 1929, p. 175). The spiral commences a short distance from the capsule; it does not expand at its distal end and it has only about six turns.

The very close resemblance between the external appearance of *D. cincta* and the young of *M. dianthus* has been discussed by T. A. Stephenson (**1**, 1925, p. 884) and the differences between them enumerated. The fewer and rather larger tentacles and the purple-grey colouring round each cinclis in *D. cincta*, with the differences in the stinging cells from the acontia, are three of the easiest and most readily ascertained characters which distinguish these two anemones.

TABLE I.

MEASUREMENTS IN SEA-WATER OF THE LIVING CAPSULES OF THE UNEXPLODED SPIRULAE (SP.) AND THE EXPLODED PENICILLI (PEN.) FROM THE ACONTIA OF FIVE SPECIMENS OF *D. cincta* FROM THE RIVER ROACH AND TWO FROM PLYMOUTH.

All the anemones were small; the average diameter of the disc was 1·5 cm. and the base 0·6 cm.

Locality.	No. of Nematocysts.	Range in size in μ of the nematocysts.	Average size in μ of the nematocysts.
River Roach 1	Sp. 20 Pen. 20	15–17 × 1·5–3 42–55·5 × 7–8	16·1 × 2·3 46·5 × 7·6
,, ,, 2	Sp. 20 Pen. 20	14–17 × 2–2·5 40·5–45 × 6–7	15·1 × 2 43·7 × 6·4
,, ,, 3	Sp. 20 Pen. 20	14–16 × 2–2·5 33–44 × 6–6·5	15·2 × 2 38·4 × 6·3
,, ,, 4	Sp. 20 Pen. 20	13–15·5 × 1·5–2 35·5–44 × 5·5–7	14·7 × 2 39·7 × 6·3
,, ,, 5	Sp. 20 Pen. 20	13·5–15·5 × 1·5–3 39–43 × 6·5–8	14·8 × 2 40·5 × 7·2
Plymouth Breakwater 1	Sp. 20 Pen. 20	13–17 × 2–2·5 45–52 × 6–7·5	14·9 × 2·1 47·7 × 6·5
,, 2	Sp. 20 Pen. 20	14–17 × 2–2·5 42·5–45 × 5–7	15·7 × 2 43·8 × 6·2

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Additions to the Plymouth Marine Fauna (1931) in the Crustacean Orders *Tanaidacea, Isopoda* and *Amphipoda.*

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With 1 Figure in the Text.

THIS list contains 2 species of TANAIDACEA, 6 of ISOPODA and 28 of AMPHIPODA. These were all collected by myself in 1934–5, with the exception of 3 species of Amphipoda, which have not been entered in the Plymouth list although accounts of their capture at Plymouth have been published. These are *Eusirus longipes* Boeck, recorded by Hunt (1924); *Gammarellus angulosus* (Fabr.), by Kitching, Macan and Gilson (1934); and *Gammarus zaddachi* Sexton, by Serventy (1935).

The list is drawn up in the systematic order adopted in Plymouth Marine Fauna (1931), with a reference to a good illustration of each species. The dates and circumstances of capture are stated, and when a species has already been recorded from off the coasts of Devon and Cornwall by Norman and Scott (1906) a note to that effect has been made. The distribution is not stated, since recent accounts of the distribution of every species are available in the following works:

Tanaidacea and Isopoda: Nierstrasz and Stekhoven, 1930 (except for *Synisoma acuminatana*, q.v.).

Amphipoda: Chevreux and Fage (1925) or Stephensen (1929).

All the Amphipod species in this list are included in one or other of these publications, and almost all in both.

Every species has been referred to a specialist for identification. Tanaidacea and *Eurydice truncata* and *Gnathia oxyuræa* to J. H. Schuurmans Stekhoven of Utrecht; the other Isopoda to Prof. W. M. Tattersall of Cardiff; the Amphipoda to Dr. K. Stephensen of Copenhagen, excepting *Gammarus zaddachi* Sexton, which Mrs. Sexton herself has named. A complete set of the specimens named by these experts has been given to the Museum at the Plymouth Laboratory, and specimens of a number of species are in the British Museum (Nat. Hist.).

Order TANAIDACEA

Family **Tanaidæ.**

TANAIS CHEVREUXI Dollfus [*Dollfus*, 1897, p. 36]

28-6-34. Looe; about 30 specimens making burrows in the silt in crevices of shale from about half-tide downwards.
5-1-35. Wembury; in similar situations, a few ♀♀ only.

As far as my collecting experience goes the habitat of this species is quite distinct from that of the far commoner *T. cavolini* M. Edw. I have found *T. chevreuxi* nowhere but in shale crevices; and *T. cavolini* very commonly in old borings of Limnoria in Millbay West Wharf, and in burrows, apparently of its own making, in the felting of sandgrains formed round a red alga (*Polysiphonia* sp.) on rocks near high-tide mark (Salcombe, Wembury, Rum Bay).

LEPTOGNATHIA GRACILIOIDES (Lilljeborg) [*Nierstrasz* and *Stekhoven*, 1930, p. 152]

16-5-35. 1 mile S. from Plankton Station L3, 20–25 fm., 5 ♀♀.
6-7-34. Cawsand Bay, 3–5 fm., 5 ♀♀.

The best account of the boreal species of Leptognathia is given by Hansen (1913, pp. 65 *et seq.*). According to him *L. gracilioides* has been confused with three other species, all more northerly in distribution: namely *L. gracilis* Kröyer, *L. sarsii* Hansen and *L. longiremis* Lilljeborg, all of which he figures. The figures labelled *L. longiremis* in Sars (1885) and Sars (1896) are said by Hansen to refer to *L. gracilis* and *L. sarsii* respectively. *L. gracilioides* has never been figured, so I have drawn the cheliped of a ♀ from the locality south of L3 (Fig. 1).

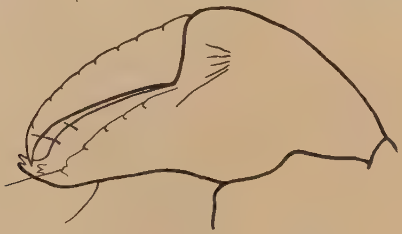

FIG. 1.—*Leptognathia gracilioides*, cheliped of ♀, × 190.

The thumb is bifid at the tip and smooth along the anterior edge. On its outer surface it bears a longitudinal tuberculated ridge. All my specimens agree in these respects.

In the other three species the thumb is single at the tip, and the distal part of the anterior edge bears four or five sharp serrulations. Tubercles are present on the thumb in *L. sarsii*, though not in *L. gracilis* and *L.*

longiremis, but this species is easily distinguished by the presence of a triangular projection on the lower lateral edge of the last abdominal segment, which is absent in all the other three species. This is well shown in the figures of Sars (1896).

Order ISOPODA

Sub-Order FLABELLIFERA

Family **Anthuridæ**

CYATHURA CARINATA (Kröyer) [*Norman* and *Stebbing*, 1886, p. 124]

1-8-34. R. Lynher, Wivelscombe Lake; 1 specimen in "salting cliff" (apparently an unusual locality).
6-6-35. R. Lynher, opposite Sconner Creek; 6, in mud.
3-7-35. R. Tavy, Maristow Ford; 8, in mud on R. bank.

There is little doubt that the specimens from Tamar mud-flats recorded by Percival (1929, p. 102) as *Anthura gracilis* (Montagu), and entered as such in Plymouth Marine Fauna (1931), are really *Cyathura carinata*, though they are not available for examination. *Anthura gracilis* is usually found in dredgings of stone and weed, and scarcely enters brackish water.

Cyathura carinata has been recorded in English estuaries in Norfolk by Gurney (1907), Suffolk by Serventy (1935), and Hampshire by Omer-Cooper (1916). I have also found it in the Exe and Taw (Devon). Apparently it is common and widely distributed in England.

Family **Gnathiidæ**

GNATHIA OXYURÆA (Lilljeborg) [*Monod*, 1926, p. 538]

16-5-35. 4 ♂♂, 3 ♀♀ among tubes of *Chætopterus variopedatus* trawled about 10 miles S. of the Eddystone in about 35 fm.

Recorded by Norman and Scott (1906) from near Starcross, S. Devon, in 5 fathoms.

Family **Cirolanidæ**

CIROLANA BOREALIS Lilljeborg [*Sars*, 1897, p. 70]

25-10-34. Mallard Buoy, Sound, 1 dredged.
4-12-34. Melampus Buoy, Sound, 1 dredged.

Recorded by Norman and Scott (1906) as rare off Devon coast.

EURYDICE TRUNCATA (Norman) [*Norman*, 1868, p. 421]

4-9-34. Eddystone Shell Gravel, 2 dredged.

Recorded by Norman and Scott (1906) off Prawle Point, Devon.

Sub-Order VALVIFERA

Family **Idoteidæ**

IDOTEA VIRIDIS (Slabber) [*Sars*, 1897, p. 83, as *I. viridis*; Plate 34 as *I. angusta*]

1-8-34. A large number of ♂♂ and breeding ♀♀ from Wivelscombe Lake, on the R. Lynher.
31-5-35. The same locality, common among Ulva in salting pools.

The species is also common among the Zostera in St. John's Lake, according to T. G. Tutin who has brought me back specimens.

Sars states that the colour is uniformly greenish. A large proportion of the living specimens that I have seen are dark greenish brown or clear green dotted with black.

SYNISOMA ACUMINATANA Leach [*Dollfus*, 1894, p. 5]

5-4-35. Wembury Bay West, about 12 specimens washed from *Halidrys siliqua* in a large pool at about half-tide level. The ♀♀ were ovigerous, and ♂♂ were present.

These were kept alive for two months in the Laboratory where they fed voraciously on Halidrys. At rest they ranged themselves along the stalks or vesicles, and showed such resemblance to the vesicles in colour, form and size, that they were difficult to distinguish.

According to Norman and Scott (1906) this species has been recorded from Devonshire by Leach, and Cornwall (Falmouth) by Cocks.

Distribution. Mediterranean and Adriatic, Black Sea, S. British coasts to Cumbrae on the Clyde, Channel Isles. Collinge (1917, p. 752).

Family **Lyssianassidæ**

LEPIDEPECREUM LONGICORNE (Bate and Westwood) [*Chevreux* and *Fage*, 1925, p. 63]

17-10-34. Cawsand Bay, D.-net, 1 ♀.
1-2-35. Tow-nets, 1 juvenile.
19-2-35. Ring-trawl, 2 ♀♀.

The specimens in the tow-nets and ring-trawl were attached to pieces of hydroid, and had probably been brought up from the bottom by rough weather.

Family **Ampeliscidæ**

AMPELISCA DIADEMA (A. Costa) [*Chevreux* and *Fage*, 1925, p. 82]

I have dredged this species rather commonly, on mixed grounds with a high silt content, in 20–25 fathoms. *A. tenuicornis* Lilljeborg was found, usually in much greater numbers, in the same hauls. No doubt this name has frequently been applied to both species.

Family **Argissidæ**

ARGISSA STEBBINGI J. Bonnier [*Chevreux* and *Fage*, 1925, p. 90]

17-10-34. Cawsand Bay; 1 ♂, 1 ♀ with eggs.
29-11-34. Middle Sound; 2 ♀♀ with eggs.
29-11-34. Melampus; 4 ♂♂, 3 ♀♀, 1 juvenile.

Dr. Stephensen writes, " Though eyes are present, I have referred the specimens to this species, for the hind corner of 3rd metasome segment is rounded (as in Chevreux and Fage, 1925, fig. 82), not somewhat quadrate as in *A. hamatipes* (G. O. Sars, 1894, pl. 48) (but Bonnier (1896) says that this corner is ' à peu près droit '). Nevertheless I have not been able to find other or more valid specific characters."

The presence or absence of eyes cannot be considered as a specific character in our present state of knowledge of these two species, since Chevreux and Fage state of *A. Stebbingi*, " Yeux formés de 4 à 8 cristallins disposés en carré (aveugle dans les grands fonds)."

Argissa hamatipes (Norman) is recorded by Norman and Scott (1906) off Exmouth.

Family **Haustoriidæ**

UROTHOË GRIMALDII Chevreux, var. POSEIDONIS Reibisch. [*Reibisch*, 1905, p. 163; *Chevreux* and *Fage*, 1925, p. 100, as var. *inermis*]

This species is common in clean sand at low-water springs on the east side of the river at Salcombe, just south of Millbay. It burrows to a depth of 8–12 inches at low tide.

This ground is full of *Echinocardium cordatum* and *Acrocnida brachiata*. Urothoë showed a pronounced tendency to live in the burrows of Acrocnida.

Found commonly, on 6-3-35, 4-4-35 and 2-5-35.

UROTHOË BREVICORNIS Bate [*Chevreux* and *Fage*, 1925, p. 100]

21-8-1900. D-net on the Bar, Salcombe, 2 ♀♀ (in Plymouth Laboratory Museum).
5-11-34. Dredged, Whitsand Bay, one in 3–5 fm., in 1 haul.
16-11-34. Dredged, Whitsand Bay, 19, in 3–5 fm., in 6 hauls.
7-3-35. Drake's Island, 1 in sand at extreme low-water springs.

The sand in Whitsand Bay is similar to that at Salcombe in which *U. grimaldii* var. *poseidonis* occurs. That is to say when graded by the sieves specified by Allen (1899), it contains about 95% of fine sand and 0·3 to 0·5% silt.

In seven hauls taken on similar sand in Bigbury Bay no Urothoë was found.

Recorded by Norman and Scott (1906) from Goodrington Sands.

UROTHOË ELEGANS Bate [*Chevreux* and *Fage*, 1925, p. 101]

16-5-34. 1 mile S. of Plankton Station L3; 2 ♀♀.
6-7-34. Cawsand Bay; 3 ♂♂, 4 ♀♀.
14-8-34. Sand near Eddystone, 28 fm.; 1 ♀.
3-10-34. Rame–Eddystone, 25–27 fm.; 4 (2 hauls).
17-10-34. Cawsand Bay; D-net, 2.
1-11-34. Cawsand Bay; 1.
29-11-34. Melampus, Plymouth Sound; D-net, 1.
29-11-34. Melampus; 19.
12-4-35. White patches, Plymouth Sound, 1.

With two exceptions all these collections were made with the fine-meshed dredge.

This is the smallest of the four local species and lives in finer and siltier sand than any of the others. The soil of Cawsand Bay contains 78% of fine sand and 19% of silt, and the soil at Melampus is a mixture of a similar silty sand with large stones. The largest of the four local species is *U. marina* (Bate) which lives in coarse sand or fine gravel (e.g. some parts of the Eddystone shell-gravel area).

Recorded by Norman and Scott (1906) in tow-nettings off the north and south coasts of Cornwall.

Family **Amphilochidæ**

AMPHILOCHUS SPENCE-BATEI (Stebbing) [*Chevreux* and *Fage*, 1925, p. 115]

29-11-34. Melampus; D.-net, 2.
29-11-34. Asia Shoal; D.-net, 6.

Family **Leucothoidæ**

LEUCOTHOË INCISA D. Robertson [*Chevreux* and *Fage*, 1925, p. 123]

30-3-33. Eddystone; stramin-net, 1 ♂. Collected by F. S. Russell.

LEUCOTHOË LILLJEBORGI Boeck [*Chevreux* and *Fage*, 1925, p. 124]

14-8-34. Rame mud, 20–25 fm.; 13.

Besides these a number of juvenile or incomplete specimens belonging possibly to one or other of these species were taken in Cawsand Bay, New Grounds, Melampus, Bigbury Bay and the Eddystone Grounds.

Also among tubes of *Chætopterus variopedatus* trawled 6–10 miles south of the Eddystone, ten specimens were obtained on 16-5-35, and six on 23-9-35, of a large undescribed species of Leucothoë.

Family **Stenothoidæ**

PARAMETOPA KERVILLEI Chevreux [*Chevreux* and *Fage*, 1925, p. 138]

7-10-34. Cawsand Bay; D.-net, 1 ♀ with eggs.

Family **Acanthonotozonidæ**

PANOPLOEA EBLANÆ (Bate) [*Chevreux* and *Fage*, 1925, p. 149]

1-2-35. Tow-nets, 1.

Family **Calliopiidæ**

CALLIOPIUS CRENULATUS Chevreux and Fage [*Chevreux* and *Fage*, 1925, p. 183]

6-3-35. Salcombe; washed from *Cystosira* sp. just below extreme low-water springs, 1 ♀ with eggs.

I have found *C. læviusculus* (Kröyer) in rock-pools near low-water at Treyarnon Bay on the coast of North Cornwall, and Norman and Scott (1906) record it from Exmouth and Teignmouth Bay under the name of *C. rathkei* (Zaddach). No doubt this species exists also in the Plymouth area. Stephensen (1931, pp. 282 286) gives reasons for considering these two names synonymous.

Family **Pleustidæ**

STENOPLEUSTES MALMGRENI (Boeck) [*G. O. Sars*, 1894, p. 355]

26-7-34. Metre-net, 6 miles S. of Rame Head, 2.
2-8-34. Metre-net, 2.
22-10-34. Tow-nets, 1 ♀ with eggs (3 mm. long).
14-2-35. Tow-nets, 1 ♀ with eggs (4 mm. long).
19-2-35. Ring-trawl, 1 ♀ with eggs.

These specimens were probably brought up from the bottom by rough weather.

Sars (1894) described his specimens, which came from deeper water (80–150 fathoms) and from further north, as colourless. Mine were quite brightly coloured (e.g. specimen of 14-2-35 described from life):

"*Eyes*: red pigment lying deep in the centre, circumference and surface colourless. *Antennæ*: colourless and transparent, except for the two basal joints which are strawy-brown; distal end of joints ringed with red-brown dots. *Body*: colourless, with much underlying strawy-brown pigment, and a few superficial red-brown or orange-brown dots."

My adult ♀♀ measured only 4 mm., whereas his were 7 mm. long.

Family **Eusiridæ**

EUSIRUS LONGIPES Boeck [*Chevreux* and *Fage*, 1925, p. 201]

14-8-34. Rame mud; 1 specimen 4·5 mm. long.
14-8-34. Rame, Turitella ground; 1 specimen 10·5 mm. long with eggs, 1 specimen 9 mm. long.

This species was first found off Plymouth by O. D. Hunt (1924, p. 580), but it has not been included in Plymouth Marine Fauna.

Family **Gammaridæ**

GAMMARELLUS ANGULOSUS (Rathke) [*Chevreux* and *Fage*, 1925, p. 204]

Wembury Bay, identified by G. A. Steven. See Kitching, Macan and Gilson (1934, p. 699).

Recorded as *Amathilla homari* by Norman and Scott (1906) from Torquay and Ilfracombe (Devon), and Falmouth, Fowey and Polperro (Cornwall).

GAMMARELLUS HOMARI (Fabricius) [*Chevreux* and *Fage*, 1925, p. 205]

6-3-35. Salcombe. Washed from *Cystosira* sp. just below extreme low-water springs. 4 immature specimens.

MELITA PELLUCIDA G. O. Sars [*Chevreux* and *Fage*, 1925, p. 228]

Occurs in a few streams running into the Tamar and Tavy.

13-6-35. R. Tamar, stream through Haye, about 2 m. below Calstock bridge ; abundant.
3-7-35. R. Tavy, stream at Lopwell ; common.
do. Lopwell ferry, in channel ; a few.
do. Blaxton creek, in channel ; a few.

In all these localities *Gammarus chevreuxi* Sexton and *G. zaddachi* Sexton also occurred abundantly. All were in water of low salinity. At Lopwell Ferry and in Blaxton Creek the salinity rises considerably at high tide ; but the other two streams are separated from the main current by valves, and the water must always be nearly fresh.

I have also found this species in the Exe (S. Devon), Taw (N. Devon) and Benfleet Creek (Essex) in similar situations. The only other English locality known for this species is Norfolk, Gurney (1907).

GAMMARUS ZADDACHI Sexton [*Sexton*, 1912, p. 657]

In March, 1934, a number of specimens of *G. zaddachi* were found in the River Tamar among Fucus at Pentillie Quay, Haldon Quay, and Whitsam by Serventy (1935), who also records the species from Suffolk and Norfolk.

In 1935 I found it to be the commonest brackish-water Gammarus in the Tamar, Tavy and Lynher. It was common in nearly every stream running into these rivers that I investigated, and in the upper tidal reaches of the Tavy from Mount Jessop Ford to Lopwell Ferry.

Percival (1929) in his report on these estuaries does not record it, including it probably under *G. locusta* or *G. duebeni*.

I have also found it in brackish water in the Camel (N. Cornwall), Exe (S. Devon), Taw (N. Devon), Frome (Wareham, Dorset), Avon (Tewkesbury, Gloucestershire), Towy (S. Wales).

Family **Dexaminidæ**

DEXAMINE THEA Boeck [*Chevreux* and *Fage*, 1925, p. 265]

This species is common among weeds, and roots of Laminaria near low-water mark on the rocks below the Laboratory. I have also found it at Looe, at Wembury and on the Salstone.

Recorded by Norman and Scott (1906) from Exmouth, Dartmouth, Falmouth.

Family **Talitridæ**

HYALE PERIERI (Lucas) [*Chevreux* and *Fage*, 1925, p. 284]

12-4-35. Gara Point among *Nucella lapillus* on an exposed headland ; 4.

These specimens include an adult ♂ and a ♀ with eggs ; owing to their small size (*ca.* 4 mm.) Dr. Stephensen has tentatively included them under var. *minor* Chevreux and Fage. Some specimens which I collected in exposed situations on the North Cornish Coast at Trevose Head, Treyarnon Bay and Trevarrian are larger than these, and agree in size with the species *H. perieri* as described by Chevreux and Fage.

Two other Hyale species are present on the S. Devon coast. *H. nilssoni* (Rathke) is very common intertidally in areas which are moderately or very sheltered (e.g. Plymouth Breakwater, Wembury, Looe, Tamar Estuary to beyond Saltash). *H. pontica* (Rathke) has so far only been found near low-tide mark on the Breakwater—a position apparently intermediate in exposure between those inhabited by the two other species.

Family **Photidæ**

GAMMAROPSIS NANA G. O. Sars [*Sars*, 1894, p. 561]

29-11-34. Melampus ; D.-net, 1 ♂, 1 ♀.
29-11-34. Asia Shoal ; D.-net, 6 ♀♀.
18-2-35. Tow-nets, 1 ♂, 3 ♀♀.
19-2-35. Ring-trawl 1 ♀.

Stebbing (1906) and Chevreux and Fage (1925) considered this species the same as *Eurystheus palmatus* (Stebbing and Robertson) [Chevreux and Fage, 1925, p. 313]. But Dr. Stephensen advises me to record it under Sars' name, believing the species to be possibly distinct. The 2nd gnathopod of the ♂ is slightly different.

PODOCEROPSIS SOPHIÆ Boeck [*Chevreux* and *Fage*, 1925, p. 316]

4-5-34. Mewstone Grounds ; 1 on *Maia squinado.*
16-5-34. 1 mile S. of Plankton Station L3 ; 1 ♂, 6 ♀♀.
18-7-34. Mixed grounds off breakwater light, 23 fm. ; 1 ♂, 1 ♀.
2-8-34. Metre-net (rough weather) ; 1 ♂, 3 ♀♀.
3-10-34. Rame–Eddystone, 27 fm. ; 1 ♀.
22-10-34. Tow-nets, 1.
18-2-35. Tow-nets, 1 ♂, 3 ♀♀.

This species is quite common on mixed grounds with much silt.

Recorded by Norman and Scott (1906) from Start Bay.

Leptocheirus pilosus Zaddach [*Chevreux* and *Fage*, 1925, p. 322]

29-1-35. Neille Point, R. Tamar; one.
2-8-35. Whitsam, R. Tamar, several among *Cordylophora lacustris.*
9-8-35. Chelson Meadow in ditches near sluice; several building nests on *Ruppia marina.*
3-9-35. Calstock Bridge and Ashburton Turn, R. Tamar; abundant among *Cordylophora lacustris.*

I have also found this species in similar situations in the Exe (S. Devon), Taw (N. Devon) and Towy (S. Wales). It is recorded from Suffolk by Serventy (1935) and from Norfolk as *Leptocheirus* sp. by Gurney (1907).

Leptocheirus pectinatus Norman [*Chevreux* and *Fage*, 1925, p. 324]

3-10-34. Rame–Eddystone, 25 fms.; 2 ♀♀.
29-11-34. New grounds, Plymouth Sound; 1 ♀.

A third species, *Leptocheirus guttatus* (Grube), is recorded from Falmouth harbour by Norman and Scott (1906), and probably is also present at Plymouth.

Family **Amphithoidæ**

Amphithoë vaillanti Lucas [*Chevreux* and *Fage*, 1925, p. 333]

6-7-34. Cawsand Bay; 36.
9-8-34. New grounds; 2.
14-8-34. Near Drake's Island; 1.
11-10-34. Mouth of R. Yealm; 9.
18-10-34. Winter Shoal; 32.
2-11-34. Rame mud (20–25 fm.); 3, on a *Maia squinado.*
29-11-34. Middle Sound; 2.
7-12-34. Winter Shoal; 1.

With one exception (noted above) all these collections were made among algæ in sheltered shallow water (3–10 fm.). No doubt this species has frequently been confused with *A. rubricata* (Montagu) which is rather commoner in similar situations, and in addition occurs between tide marks.

Family **Corophiidæ**

Corophium acutum Chevreux [*Chevreux* and *Fage*, 1925, p. 366]

Very common among algæ, sponges and Laminaria roots just above and below low-water springs, along the fringes of Plymouth Sound; common among sponges on West Wharf and the Pontoon, Millbay Docks.

Corophium acherusicum Costa [*Chevreux* and *Fage*, 1925, p. 368]

Very common on buoys and rafts in Plymouth Sound and the Hamoaze: Tinside bathing raft, buoy off Trevol Quay St. John's Lake, buoys at junction of Tamar and Lynher, Neille Point buoys.

Sub-order HYPERIIDEA

Family **Hyperiidæ**

HYPEROCHE MEDUSARUM Kröyer [*Chevreux* and *Fage*, 1925, p. 405, as *H. kröyeri* Bovallius]

29-1-35. Tow-nets, 1 ♀ with eggs.
20-3-35. Tow-nets, 1 ♀.
4-4-35. Ring-trawl, 1 ♂.

The synonymy of this species is elucidated by K. Stephensen (1923, p. 13). From his summary of records of its occurrence it appears that Plymouth lies on the extreme south-eastern limit of its range.

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On Rearing the Hydroid *Zanclea implexa* (Alder) and its Medusa *Zanclea gemmosa* McCrady, with a Review of the Genus *Zanclea*.

By

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With 12 Figures in the Text.

Descriptions of the hydroid *Zanclea implexa* (Alder) in British waters have been given by the following authors, Alder (1857, as *Tubularia implexa* and *Coryne pelagica*), Allman (1859, as *Coryne Briareus*), Strethill Wright (1859) and Alder (1862 as *Coryne implexa*), Allman (1864 as *Zanclea implexa* and 1872 as *Gemmaria implexa*) and Hincks (1872, as *Zanclea* (*Gemmaria*) *implexa*). All these descriptions have been based upon full grown colonies in which the hydranths had a perisarc on the hydrocaulus.

We have recently had the opportunity of following through the complete development of a colony of Zanclea and have reared the medusæ to an adult stage. During their course of development both the hydroid and medusa undergo changes which have systematic importance. For this reason it is worth giving an account of our observations in some detail.

The Hydroid.

On February 3rd, 1936, a small piece of the basal stem of a colony of *Eunicella verrucosa* dredged from the Eddystone grounds was placed in a bowl of pure sea water. This had on it a small colony of an encrusting polyzoan. On February 6th there appeared growing out from this colony minute columnar stalks, which four days later developed at their apices five small protuberances (Fig. 1, A). These outgrowths grew into short capitate tentacles and at the same time a few scattered tentacles were developing from the sides of the body so that by February 11th the hydroid had assumed the appearance shown in Figure 1,B. This hydroid was very minute and extensile, and when fully extended measured about 1·5 mm. in length. The hydroid appeared to spring from a naked stolon with no visible perisarc and no trace of a hydrocaulus. By the 17th the whole colony had died down, but it started to grow up again on the 19th, and on February 20th had developed to the stage last mentioned. By the 24th the hydranths had apical whorls of five tentacles and about fifteen tentacles irregularly distributed over the body. All the tentacles were capitate and the knobs of the apical tentacles slightly larger than those of the others. A creeping stolon with developing perisarc was now clearly visible in places. On February 28th some of the hydranths had six tentacles in the apical whorl, but the majority still had five. There was still no visible perisarc on the hydrocaulus. On March 4th there were about 30 polyps, all confined to the polyzoan and the proportions of those with 6 or 5 apical tentacles was about 1 to 2. There were still about 15 tentacles on the body. By March 15th it was evident that the hydroid was a species of Zanclea ; the number of tentacles now varied from 20 to 26 in all, and the hydranths were about 3·5 mm. in length when fully extended (Fig. 2). It was noted that it " differs from *Zanclea implexa* by its smaller size, fewer tentacles, and absence of perisarc on the hydrocaulus."

By the 23rd the polyps had grown considerably in size ; they were now very tall and extremely extensile, reaching a length of nearly 10 mm. (See Fig. 3). There were about 40 tentacles in all. At the same time many had developed short ringed perisarc on the hydrocaulus. The hydranth was almost perfectly cylindrical in shape, only broadening slightly in the region from which the apical whorl of 6 tentacles sprang. The endodermal core of the hydranth was red and the proboscis white. The colony had now been growing for six weeks, when on March 24th very small polyps were noticed springing up amongst the others. In these the tentacles were reduced in size and number ; they were short and there were only 10 to 12 tentacles on the hydranth body some of which were mere knobs. Below the tentacled region of the hydranth small medusa buds were developing. An individual drawn on March 26th had four large buds, approximately radially disposed, each with a smaller bud on its supporting pedicel. A drawing of a portion of the colony as it appeared on March 28th is given in Figure 3.

On March 30th some of these medusiferous polyps were nearly as long as the original vegetative polyps, but the tentacles were stunted and reduced in number. There were no tentacles below the medusa buds. On April 1st the first medusæ were liberated and identifiable as *Zanclea implexa* (after Allman, 1872). For many weeks after this medusæ were being produced and the medusiferous polyps showed considerable variation. In some the medusa buds were arranged in a fairly compact whorl ; in others they were much more scattered, though always below the tentacles. In some the tentacular portion of the hydranth was much reduced so

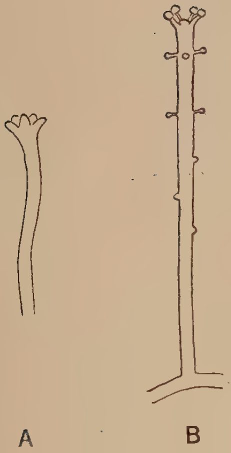

FIG. 1.

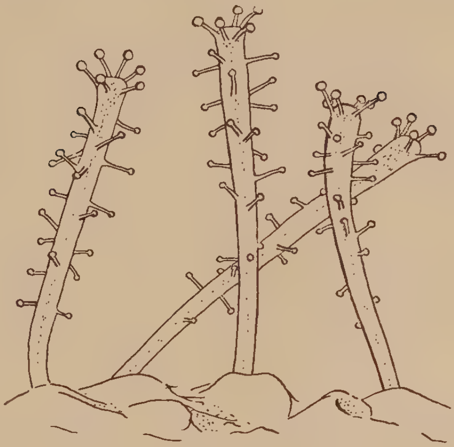

FIG. 2.

FIG. 1.—A. First appearance of developing hydranth of *Zanclea implexa* ; Plymouth, 10.ii.36.

B. Early stage of hydranth of *Zanclea implexa*, 1·25 mm. in height; Plymouth, 11. ii.36. Del. F.S.R.

FIG. 2.—Portion of young colony of *Zanclea implexa*, hydranths 3 mm. in height; Plymouth, 15.iii.36. Del. F.S.R.

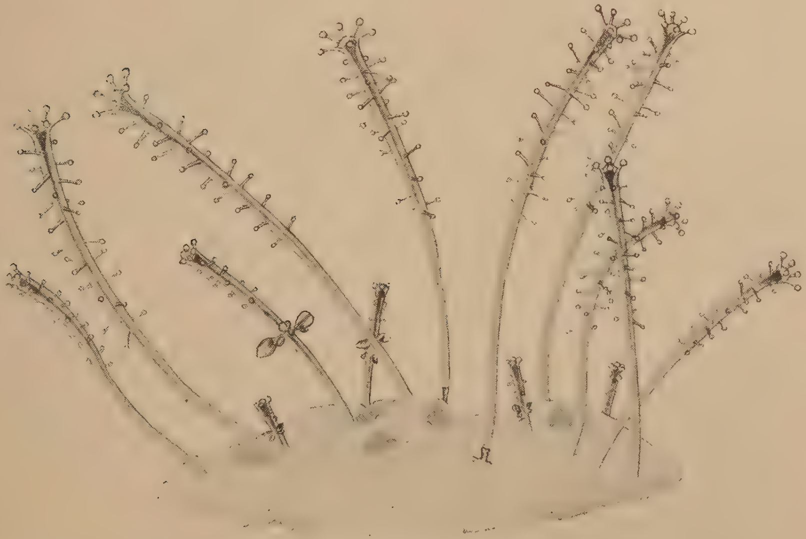

FIG. 3.—Portion of colony of *Zanclea implexa*, height of longest polyp, *ca.* 10 mm.; Plymouth, 28.iii.36. Del. F.S.R.

that there were only about 8 tentacles and the basal portion of the column was thicker ; in extreme cases the polyps were reduced to mere blastostyles (see Fig. 4). On April 20th some of the medusiferous polyps, now 10 mm. long when fully extended, appeared to be regenerating into normal vegetative polyps ; those which had liberated all their medusæ had tentacles increasing in number and size, and others on which there were still medusa buds had tentacles developing below the buds (Fig. 4). The whole colony had now increased considerably in size and was spreading over the substratum around the Polyzoan colony. The perisarc on the hydrocaulus was now quite distinct. The colony lived on producing medusæ in great numbers, but apart from noting that the colony tended to die down and regenerate in the middle of May little further attention was given to it for a time beyond keeping it supplied with food. The development of perisarc was still proceeding strongly and measurements of the hydrocaulus on May 30th gave the following results.

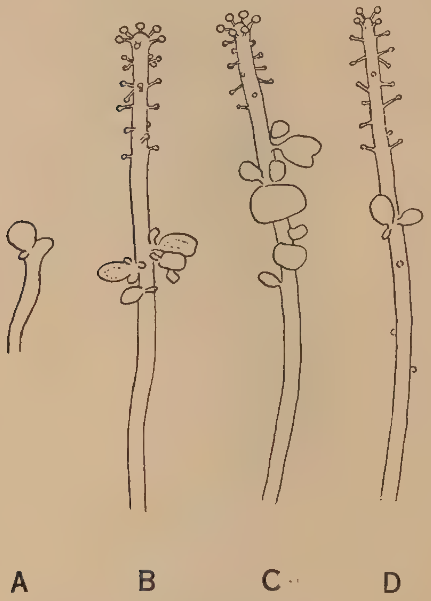

Fig. 4.

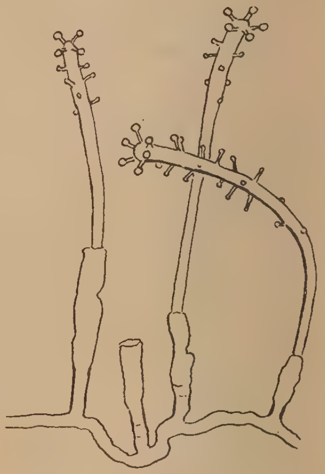

Fig 5.

Fig. 4.—Showing different types of medusa bud formation, in colony of *Zanclea implexa*, Plymouth. A, C, 4.iv.36 ; B, 30.iii.36 ; D, 20.iv.36. Del. F.S.R.

Fig. 5.—Portion of old colony of *Zanclea implexa* regenerating, 2·5 mm. in height ; Plymouth, 10.vii.36. Del. F.S.R.

Length of perisarc in mm.	0·4	0·7	0·45	0·5	0·6
Width of perisarc in mm.	0·17	0·19	0·14	0·16	0·15

One individual had a hydrocaulus with perisarc 1 mm. long.

The production of medusæ continued throughout June. On July 7th after much of the colony had died down new small polyps were developing in the old perisarc tubes, so that they now appeared as in some of the earlier figures (Fig. 5) but with pronounced perisarc on the hydrocaulus.

The colony, which had been kept in a beaker in which the water was agitated since February 13th, was still alive in October.

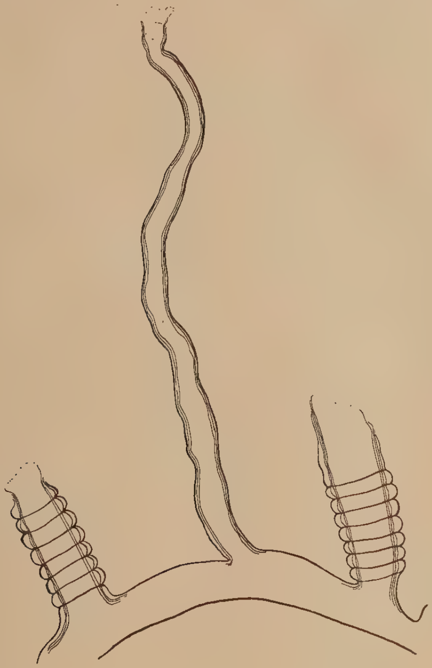

FIG. 6.

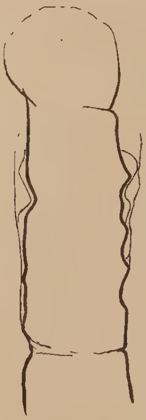

FIG. 7.

FIG. 6.—Portion of perisarc of old colony of *Zanclea implexa*, showing annulation at base of hydrocaulus; Plymouth. Del. W.J.R.

FIG. 7.—Perisarc of hydrocaulus of regenerating hydranth of *Zanclea implexa*, showing new perisarc forming inside old perisarc membrane; Plymouth, 12.vii.36. Del. F.S.R.

The hydroid had the three types of nematocysts described by Brückner (1914), namely large and small oval nematocysts, and large elongated bean-shaped nematocysts. These latter were situated in the hypostome region.

Measurements of the nematocysts gave the following dimensions:

	Average length.	Average breadth.
Small oval	0·007 mm.	0·006 mm.
Large oval	0·013 ,,	0·012 ,,
Large elongated	0·021 ,, *	0·008 ,,

* Range, 0·020–0·024.

The *perisarc*. In the earliest stages there is no visible perisarc. All perisarc must begin as a thin transparent membrane which gradually becomes thickened and visible as a horn-coloured layer. In older individuals the perisarc was well developed both on the hydrorhiza and on the hydrocaulus. The hydrocaulus which grows off approximately at right angles to the hydrorhiza is sometimes strongly ringed at its base (Fig. 6). Above the annulation the hydrocaulus continues as a simple tube often irregularly corrugated and at its upper end the perisarc becomes membranous and transparent as this region is the last to develop. Several authors (see page 119) have remarked on the appearance of an outer periderm separated from the main perisarc. The development of this outer sheath is probably as follows. During the course of the growth of a colony, the polyps frequently die down. A perisarc skeleton is thus left having at its upper end the thin membranous mouth of developing perisarc. A new polyp now grows up within the tube, and as it grows develops a new perisarc. This grows up beyond the old tube, becoming thickened at its lower end. This thickened region thus comes to lie within the upper membranous perisarc of the old tube. In this way the appearance of an outer periderm is produced, which is in reality the last perisarc to be developed by the old polyp before it died down (Fig. 7).

The fact that this colony first appeared in association with a polyzoan led to the supposition that other colonies of Zanclea might be found by obtaining polyzoa. Accordingly a small piece of encrusting polyzoan, *Cellepora avicularis* Hincks,* dredged near Stoke Point on March 17th was placed in a finger bowl. On March 20th a colony of Zanclea was found to be developing, and its course of development differed somewhat from that just described. It had evidently already passed through its vegetative stage.

The polyps first appeared as short knobbed projections of a pink colour, on the surface of the polyzoan. On development each polyp had an apical whorl of six tentacles, and a few scattered tentacles on the body (Fig. 8, A). After three days they were about 0·5 mm. in height (Fig. 8, C). On March 27th the first medusa buds appeared in a whorl below the tentacles, which now numbered 15 to 20. No perisarc was visible on any polyp. As the medusa buds grew, the upper tentacled portion of the hydranth became gradually reduced, in some the tentacles were absorbed and the body of the hydranth above the medusa buds became shorter and thinner until the hydranth was reduced to a mere blastostyle (Figs. 8, E G and Fig. 10). The first medusæ, 10 in number, were liberated on April 3rd and 20 to 30 medusæ continued to be liberated daily until the 20th of the month. Shortly after the first medusæ appeared

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* We are indebted to Miss A. B. Hastings of the British Museum (Natural History) for the identification of this polyzoan.

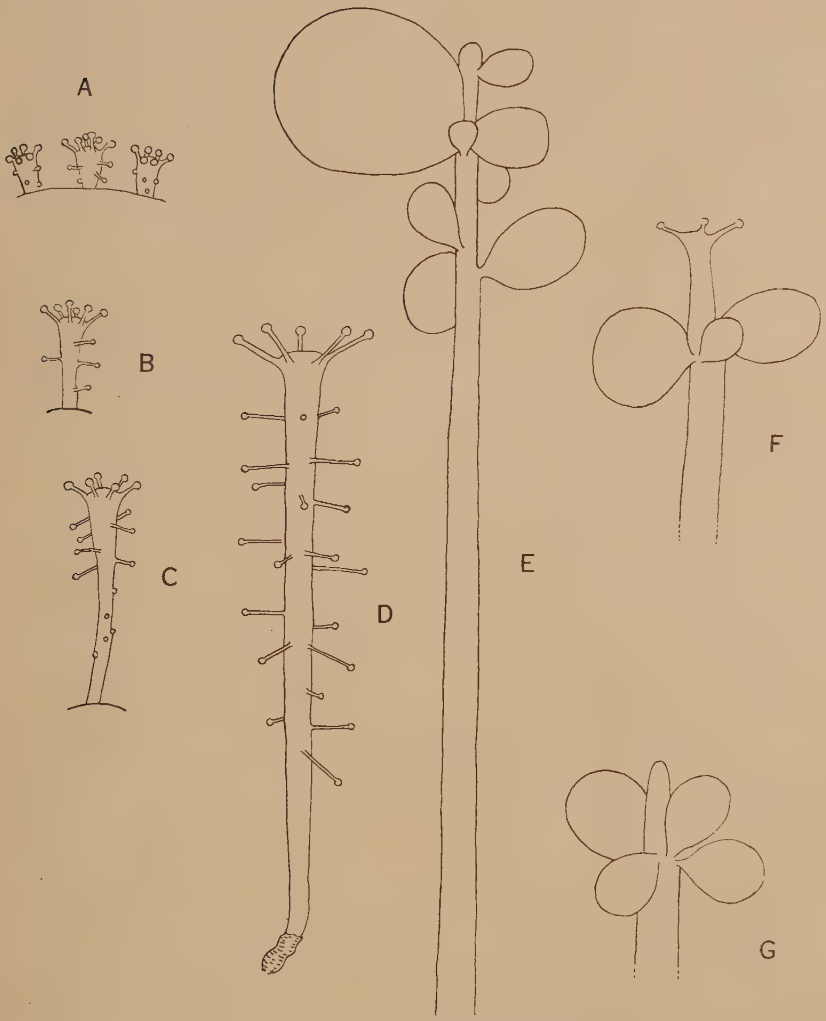

FIG. 8.—A, B, C, D. Various stages of development of the vegetative hydranths of the second colony of *Zanclea implexa*, Plymouth.

A, first appearance of the hydranths, 20.iii.36; B, a single hydranth two days later, 22.iii.36; C, a single hydranth, 23.iii.36; D, a fully developed hydranth with developing perisarc, 26.vi.36.

E, F, and G, various types of medusa bud formation, 17.iv.36. Del. W.J.R.

the blastostyle stems elongated considerably and many polyps reached a length of 2 mm. (Fig. 9). At first the medusa buds developed more or less in a whorl around the stem, but later two or even three whorls were developed (Fig. 8, E). The majority of the medusa buds had a very short stalk and younger buds rarely developed from this stalk. On the final liberation of their medusæ the blastostyles seemed to disappear overnight and by April 22nd the majority had died down. Two or three days after the disappearance of a blastostyle a very short hydranth developed in its place which developed medusa buds two days later. By April 27th all the original blastostyles had died down and the new set of polyps were differentiated into longer and shorter individuals. The shorter polyps, 0·4 mm. in height, were more numerous and developed medusa buds; the longer polyps, 1 mm. in height, were sterile. On April 30th all the reproductive polyps had increased in length and were similar in appearance to the original series already described. The vegetative polyps had now grown to a length of 1·8 mm. By May 5th all the vegetative polyps also produced and liberated medusæ for a few days, but never became reduced to simple blastostyles. More new polyps were observed growing up on May 8th; these produced two whorls of medusa buds and were only slightly reduced from the vegetative type on the 10th. By this time other polyps growing up since the 8th were only slightly longer than the original

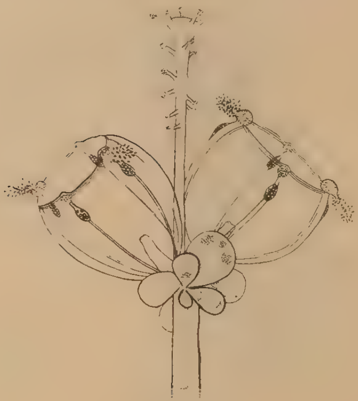

Fig. 9.

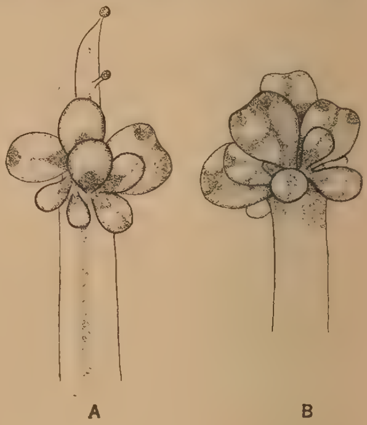

Fig. 10.

Fig. 9.—Portion of a single hydranth of second colony of *Zanclea implexa* 2·4 mm. in height, showing medusa buds and a slight reduction of the upper portion of the hydranth; Plymouth, 3.iv.36. Del. W.J.R.

Fig. 10.—A, Hydranth of second colony of *Zanclea implexa* with medusa buds almost completely reduced to a blastostyle; Plymouth, 27.iii.36.
B, Hydranth of second colony of *Zanclea implexa* completely reduced to a blastostyle; Plymouth, 27.iii.36. Del. W.J.R.

polyps and developed medusa buds by May 15th; all these latter were completely reduced to blastostyles by May 30th, and new shorter polyps were growing up. This cycle was repeated three times during the month of June. Until June 25th the colony had been kept in a finger bowl in still water and there had been no visible perisarc on any polyp. It was then transferred to a beaker in which the water was agitated and after about a week a thin perisarc was seen to be developing round the bases of the polyps (Fig. 8, D.).

It is to be noted that this colony differed slightly from the colony first described in that the hydranths were shorter and there was a much greater tendency to reduction to a complete blastostyle. A section of the polyzoan colony showed the stolon penetrating deeply into the colony.

The association of this hydroid with a polyzoan is of interest and it appears to be a very frequent habit*. Hastings (1930 and 1932) has brought together observations of such associations and it is of interest to reproduce here a remark made by Hargitt (1908). He records that the hydroid may be found at Woods Hole on a variety of objects such as shells of Mytilus and Pecten, Serpulid tubes, pebbles, water-logged wood and floating Sargassum, but adds "In one particular, however, there has been an interesting uniformity in every case which has come to my notice, namely, the colonies are invariably associated with encrusting polyzoa, usually *Schizoporella* or *Membranipora*." It would appear that polyzoa may be one of the normal settling grounds for the larval stages of the hydroid, but that in many instances as the colony grows older the stolon creeps away onto the surrounding substratum. Stechow (1911) records it on the foot of a Holothurian.

THE MEDUSÆ.

When first liberated the medusæ agreed closely in general appearance with Allman's figure (1872, Plate VII, Fig. 3). The umbrella was bell-shaped, 0·6 to 0·7 mm. in height and nearly of the same width. The jelly was uniformly thin. The margin of the umbrella was somewhat square. The four perradial exumbrella nematocyst chambers extended over the surface of the exumbrella for slightly less or more than a third of its height and were connected with the tentacular and non-tentacular bulbs by a narrow channel. The numbers of nematocysts varied considerably from 4 to 17, generally 10 to 12, in the dilated portion, to 0 to 4 in the channel itself. These nematocysts were generally more numerous in the chambers on the tentacular radii than in those on the non-tentacular radii. The stomach was cylindrical and did not exceed in length half the height of the umbrella cavity. The mouth was simple and tubular, and beset with nematocysts up to about 15 in number. The four radial canals and ring-canal were narrow, and a few large nematocysts, probably from the exumbrella sacs, were occasionally to be seen in the circular canal. There were two tentacles, each having up to 50 stalked capsules on their abaxial surfaces; these capsules were 0·018–0·02 mm. long by 0·013 broad and they contained 2 to 5 nematocysts, usually 3. They had vibratile cirri which gave them a characteristic trembling movement.* The elongated tentacular bulbs, and the non-tentacular bulbs were filled with nematocysts. Medusæ were occasionally liberated with no tentacles or with two tentacles greatly reduced and having only a few stalked capsules. The tentacle bulbs, non-tentacular bulbs and stomach were pale pink or yellowish in colour (Fig. 11).

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* Nine more colonies developed on Polyzoa dredged off Plymouth (Oct. 1936).

At a height of about 0·8 mm. the gonads were clearly visible as interradial swellings, and there was now more pale yellow than pink in the tentacle bulbs. In some specimens the stomach extended about three-quarters of the length of the subumbrella cavity. It is to be noted that there was a tendency for the medusæ liberated from the second colony described above to have slightly longer stomachs and more elongated exumbrella nematocyst channels. At 0·8 mm. the number of stalked capsules on the tentacles had increased, 86 being counted on one tentacle. In specimens about 0·9 mm. in height the gonads were further developed and a bright carmine diffuse spot appeared in the upper half of each tentacle bulb. In some the exumbrella nematocyst chambers had lengthened and become less sac-like, extending half-way up the exumbrella surface. Slight linear swellings were appearing in the middle region of each radial canal. At the same time minute opaque dots were visible on the umbrella surface arranged roughly in circular groups. In one specimen a narrow umbilical canal was seen.

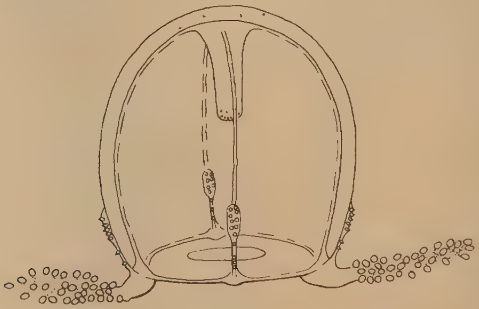

Fig. 11.—Newly liberated medusa of *Zanclea implexa*, 0·68 mm. in height; Plymouth, 1.iv.36. Del. F.S.R.

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* This movement has been observed by Allman (1872) and Murbach (1899), but was not seen by Hargitt (1904) or Brückner (1914). Among the many medusæ that we have seen, however, we have only occasionally observed it.

Great difficulty was experienced in getting the medusæ to grow; the largest specimens reached a height of 1·4 mm. They were females with few eggs, generally 1 to 3 in each interradius. In some the stomach extended nearly to the margin of the umbrella. In some the jelly of the umbrella had become thickened at its apex and in the four radii in the region of the exumbrella nematocyst channels. The shape of the exumbrella nematocyst chambers had altered, and they now had no sac-like

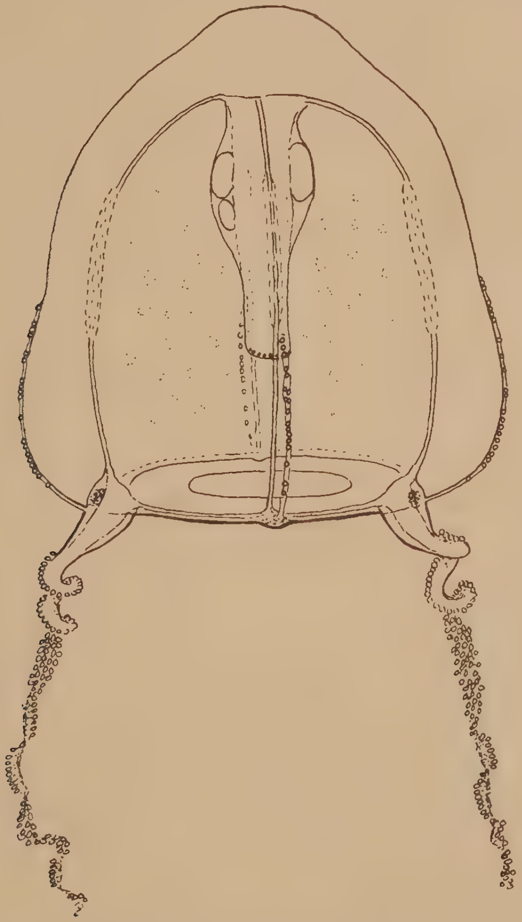

Fig. 12.—Mature medusa, *Zanclea gemmosa*, reared from the hydroid *Zanclea implexa*, 1·4 mm. in height; Plymouth, 30.v.36. The tentacles have been cut short in the drawing, and should have *ca.* 300 nematocyst capsules each. The nematocysts in the tentacle bulbs are not shown. Del. F.S.R.

dilatations, but extended upwards as linear channels for more than a third, or even than a half, of the exumbrella surface ; they contained 16 to 20 nematocysts, mostly in a single row, with occasionally two side by side. There was no indication of any increase in size of the non-tentacular bulbs. The number of stalked capsules on each tentacle had greatly increased to approximately 300 and they measured 0·022 mm. in length by 0·015 in breadth. There were distinct linear swellings along the middle portions of each radial canal, and the pattern of fine dotted circles on the umbrella was quite obvious (Fig. 12).

Discussion.

The historical literature on the synonymy of the species of Zanclea and Gemmaria is long and involved. The salient points on which differences arise appear to be as follows.

The Hydroid.

1. The European species of Zanclea has a well developed, sometimes annulated, perisarc on the hydrocaulus, as well as a perisarc on the hydrorhiza, cf., *Zanclea implexa* of British waters, *Gemmaria implexa* at Naples (Hargitt, 1904)=*Z. Hargitti* (Hartlaub, 1907)=*Z. implexa* var. *neapolitana* (Brückner, 1914). Also in ? *Gemmaria costata* from Tortugas (Mayer, 1910=*Gemmaria gemmosa* of Mayer, 1900).

The American species of Gemmaria has no visible perisarc on the hydrocaulus or hydrorhiza, cf., *Halocharis spiralis* (Agassiz, 1862), *Corynitis agassizii** (Murbach, 1899).

2. Medusa buds are borne in the proximal region of the tentacles (Allman, 1872, *Gemmaria implexa*). Medusa buds are " most numerous in a zone where the rudimentary tentacles are, though scattered ones may also be found higher up the polyp." (Murbach, 1899, *Corynitis agassizii.*)

Medusa buds are borne scattered amongst the tentacles " at any point or portion of the hydranth, and quite as frequently near the oral as the basal region of the body " (Hargitt, 1904, *Gemmaria implexa* ; and also Brückner, 1914, *Z. implexa* var. *neapolitana*). Medusa buds are borne below the tentacles (Mayer, 1910, ? *Gemmaria costata*).

3. The perisarc of the hydrocaulus in European species has an investing outer sheath or " periderm " (Alder, 1857) ; this was not seen by Allman (1872), but Brückner (1914) has shown the presence of a somewhat similar outer coat.

The Medusa.

1. The nematocyst armature on the exumbrella is present as tracks (nessel rippen) in adults (Gegenbaur, 1856, *Zanclea costata ;* Browne, 1905,

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* For a criticism of this erroneous name see Hargitt (1908).

Gemmaria implexa; Bigelow, 1909, *Zanclea gemmosa;* Mayer, 1910, Pl. 8, Fig. 6, ? *Zanclea costata.*)

The nematocyst armature on the exumbrella is present as channels ending in blind sacs (nesselpolstern) in young stages (McCrady, 1856, *Zanclea gemmosa;* Allman, 1872, *Gemmaria implexa;* Murbach, 1899, from *Corynitis agassizii;* Mayer, 1900 and 1910, ? *Zanclea costata*, Pl. 8, Fig. 3, and *Zanclea gemmosa;* Brückner, 1914, *Z. implexa* var. *neapolitana*). On these grounds Brückner separates the genera *Zanclea* and *Gemmaria.*

2. All known young stages liberated from the hydroid have only two tentacles. Adults with two tentacles have also commonly been recorded from the plankton. Medusæ with four tentacles (as in Gegenbaur's original *Zanclea costata*) may be taken in the plankton.

3. In almost all recorded specimens the mouth has no lips, but the presence of four short lips is given by Gegenbaur in his original description of *Zanclea costata.*

4. The jelly may be thin (e.g. Neppi and Stiasny, 1913), or it may be recorded as having a thickened apical process (e.g. Browne, 1905, and Hartlaub, 1907, Fig. 111).

5. There may be a peduncle above the stomach (e.g. Browne, 1905; Hartlaub, 1907, Fig. 111).

6. The stalked capsules on the tentacles are sagittate (McCrady, 1857), spherical (Mayer, 1910, Pl. 8, Fig. 7, and Vanhöffen, 1911, p. 200, Fig. 3), but in all other descriptions oval.

Let us now consider these points individually.

The Hydroid.

1. The presence or absence of perisarc has been regarded by several authors as a generic character (e.g., Hartlaub, 1907, *Zanclea* and *Halocharis;* and Stechow, 1923). We have now shown that the perisarc of the hydrocaulus and hydrorhiza is only developed with age, and is therefore not necessarily a distinguishing character between the European and American species. As regards the American hydroid Murbach (1899) incidentally adds the following footnote: "This summer I have found what appears to be a second species of *Corynitis.* It differs from *C. agassizii* in the presence of a well-developed perisarc on the hydrorhiza and the short hydrocaulus, forming imperfectly annulated cups about one fourth the length of the polyp, and in the fact that the medusa-buds are on branched stalks." This may well have been an older colony than he had seen before.

2. We have shown that the method of production of medusa buds is an extremely variable character.

3. The presence of an outer periderm over the hydrocaulus observed by Alder, was not seen by Allman. Strethill Wright (1859, p. 108) comments

as follows: "The internal layer of the corallum is brown and of horny texture; the external coat colourless and membranous. The first is frequently annulated; the second not so, but is occasionally gathered in longitudinal folds. I am disposed to think that this coat is the 'colletoderm,' or glutinous covering of the corallum (in this species highly developed and indurated), separated from the inner coat by the action of the spirit in which the specimen was immersed." Brückner (1914) says of the Naples variety that the hydrocaulus is always simple in its whole course, but occasionally the double walled protective covering is produced by a slimy gelatinous mass over the periderm which becomes separated from it as a thin layer. He would not decide whether this formation could be regarded as identical with that described by Alder. A kind of doubling was observed by Stechow* (1925, p. 23), from material "nach bei England" from the Valdivia Expedition. We have explained on page 112 how this appearance is produced with age (see also Hincks, 1872, p. 394). Altogether this character appears to be rather inconstant and of very doubtful specific value.

The Medusa.

1. We have shown that the "nesselpolstern" develop into "nesselrippen." McCrady (1857) in his original description of the genus *Zanclea* says: "The thread-cells in the older animals are arranged one by one along the row, but in the younger there is simply a cluster of them above each tentaculum." As regards *Z. gemmosa* he also says: "Their disposition in a cluster is probably a character of very young individuals, for I have found a specimen not differing much in size from the rest which had these cells arranged in a row one by one as in Gegenbaur's species."

The fact that Graeffe (1884) says that in the Mediterranean the medusa makes no metamorphosis cannot be regarded seriously in this respect as it is doubtful whether at that date he would have studied this particular point.

2. Browne (1905)† remarking on the presence of medusæ with two and four tentacles in the plankton at the same time says: "I do not think that they are distinct species, as they are similar in every detail except in the number of tentacles." This opinion was also held by Mayer (1910).

We have seen a Zanclea with four tentacles from the plankton at Plymouth (F. S. R., 19. vii. 34) which was almost the same size as the largest medusa with two tentacles that we have reared. The fact that all four tentacles were equally developed rather suggests that it was liberated from its hydroid with the four tentacles already formed. On the whole, therefore, no certain opinion can be expressed on this point until a medusa with four tentacles has been reared from a hydroid.

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* It was recorded as not seen by Stechow (1919, p. 5), but in this (1925) report he says that the species was not *G. implexa*, but rather *Sarsia pulchella* (Allman).

† The only other British records not cited are Browne (1896), Browne and Vallentin (1904), Delap, M. and C. (1905) and Robson (1914).

3. Although Gegenbaur (1856) in his original description of *Z. costata* says that the mouth has four short lips his drawing leads one to suppose that they are so slightly developed that they could hardly be termed "lips." It is possible that in large individuals the mouth corners tend to develop slightly to give this appearance. Mayer (1910) says: "The common *Zanclea* of the southern coast of New England, in America, may become mature with only 2 tentacles, and with poorly developed lips. On the other hand, a very similar medusa is occasionally found in the same waters with 4 tentacles and with 4 well-developed lips. I am inclined to believe that these conditions represent developmental stages, or starved and well-fed states of one and the same medusa."

4. We have shown that the thickness of the jelly can increase with age; this can hardly be a character of specific value.

5. Hartlaub (1907) says that the Trieste form differs from the British form in the absence of a stomach peduncle, and Neppi and Stiasny (1913) confirm this for the Mediterranean. Browne (1905) also records that the stomach is upon a short peduncle. It is doubtful to what extent this peduncle is any more than a reflection of the thickness of the apical jelly.

6. Although McCrady (1857) drew the stalked capsules of the young American medusæ with points (Agassiz, 1865, refers to them as "arrow-shaped"), Murbach drew them as ovals. There seems to be no doubt that such differences may be due entirely to inaccurate draughtsmanship. Our capsules agreed closely in outline with those drawn by Murbach (1899) and Brückner (1914). Vanhöffen (1911) divided the Zanclea species from the Valdivia Expedition into two series in which the nematocyst capsules were small spherical, and large oval, their measurements being 0·02 mm. diameter and 0·05–0·06 mm. long respectively. On the grounds that those with small capsules had long exumbrellar nematocyst canals, he regarded them as *Zanclea costata* Gegenbaur although they had but two tentacles (cf. also Mayer, 1910, Pl. 8, Fig. 7). Those with large capsules had short "Nesselpolster" and were regarded as being *Zanclea implexa* (Alder). As regards size of capsules our specimens agree with Vanhöffen's first group, although in shape they come into his second group. But the possibility that the spherical appearance may be due to contraction in the preserved state must be borne in mind. In some of our specimens on preservation the capsules appeared distinctly spherical.

A consideration of the above points leads to the conclusion that no character can be brought forward whereby the *Zanclea implexa* of the European coasts and *Gemmaria gemmosa* of the American coasts can be regarded as specifically distinct. On these grounds it seems only right that the two should be united, with perhaps the proviso that in the young medusæ of the American form the perradial nematocyst pads are usually short. In doing this it will be necessary to take the name *Zanclea implexa* (Alder) as having priority for the hydroid and *Zanclea gemmosa* McCrady for the medusa. This is assuming for the moment that the four-tentacled medusa is kept distinct as *Zanclea costata* Gegenbaur. If it should be found that at times *Zanclea implexa* produces a medusa which already has four tentacles or develops them later, then the name *Z. gemmosa* will have to give way to *Z. costata* Gegenbaur.

It would appear that *Zanclea gemmosa* is a medusa with a world-wide distribution. Bigelow (1909) recorded it from Acapulco Harbour in the Pacific, noting that the exumbrella nematocyst channels were rather longer than in McCrady's medusa. Uchida (1927) has recorded a Zanclea from Japan which "is perhaps referable to *Z. gemmosa*," . . . "but is distinguished by its smaller size, ellipsoidal shape, thick jelly and different coloration." None of these characters can be regarded as having specific value. Weill (1934, p. 422) has also recorded *Gemmaria gemmosa* from the Gulf of Siam.

The hydroid *Gemmaria gemmosa* has been recorded by Stechow (1911) from the coast of Japan; this was referred by him later (Stechow, 1923, b) to the genus *Halocharis*.

Of other records of Zanclea (or probable Zanclea) hydroids there are *Coryne sessilis* Gosse (1853, p. 208, Pl. XIV, Figs. 1–3) found in a rock pool at Capstone on the north Devon coast "from a crust of *Lepralia* . . . . close around the base of a cluster of *Cellularia avicularia*"; *Gymnocoryne coronata* Hincks (1871, p. 75, Pl. V, Fig. 1) from Salcombe, South Devon; *Coryne* vel *Syncoryne cylindrica* Kirkpatrick (1890, p. 605, Pl. XIV, Fig. 1), from Albany Passage, N. Queensland, growing with *Cellepora granulosa*; *Gemmaria nitida* Hartlaub (1905, p. 527) from Juan Fernandez; and *Zanclea protecta* Hastings (1930 and 1932) from the Tropical East Pacific and the Great Barrier Reef of Australia in association with various polyzoa.

Of these *Coryne sessilis* Gosse differs somewhat from our Zanclea in having all the tentacles arranged in whorls. Albeit his drawing shows an extraordinarily close resemblance with that by Mayer (1900) of a hydroid from which he obtained the *Gemmaria gemmosa* medusæ which he later (1910) thought might be *Z. costata*. *Gymnocoryne coronata* Hincks is almost certainly a young Zanclea in which the perisarc is not yet developed on the hydrocaulus; it differs from our Zanclea in having 8 or 9 tentacles in the apical whorl. It is doubtful whether this is a specific difference. *Syncoryne cylindrica* Kirkpatrick only differs from *Zanclea protecta* Hastings in the weaker development of perisarc. For *Z. protecta* Hastings (1930) gives the differences from other known species as "smaller number of shorter, relatively thicker tentacles, the very slight development of the perisarc, and in the gonophores, which originate directly from the hydrorhiza—not from the hydranth." The first two of these characters cannot be regarded as specific in the light of our observations, while the description of the stalks with medusa buds shows a very suggestive similarity with our blastostyles.

Hastings, however (1932), has shown that there is a difference in the nematocyst armatures of *C. cylindrica* and *Z. protecta*. While *Z. protecta* had only one kind of nematocyst, 0·009 mm. in length by 0·007 mm. in width (Hastings, 1930), *C. cylindrica* had also large nematocysts 0·032 mm. by 0·016 mm. We have shown (p. 111) that *Z. implexa* has the three types of nematocysts observed by Brückner (1914).

Hartlaub's *Gemmaria nitida* shows no specific characters to distinguish it from *Z. implexa*, but the absence of fully developed medusa buds does not allow a final opinion.

At this stage, therefore, we cannot combine all the species of Zanclea hydroids as the great difficulty of distinguishing other hydroids which produce different species of medusæ is well-known. Until the true story of the Zanclea species of medusæ is known we can go no further.

Of the medusæ other than the two tentacled *Zanclea gemmosa* McCrady and the four tentacled *Zanclea costata* Gegenbaur, there remain only *Gemmaria cladophora* Agassiz (1865), *Gemmaria sagittaria* Haeckel (1879), and *Zanclea orientalis* Browne (1916). As regards *G. cladophora* the character of the shape of the subumbrella cavity hardly seems to be specific. The unequal development of the tentacles is however interesting as being possibly an intermediate stage between the two tentacled and four tentacled medusæ. On the whole this must remain a doubtful species as must *G. sagittaria*. *Zanclea orientalis*, from the Chagos Archipelago in the Indian Ocean, has the distinguishing character of broad perradial patches of nematocysts on the umbrella margin, and until it can be shown whether this is a permanent character or not it must be kept as a distinct species. Albeit the other three uncertain specimens of Zanclea which Browne records from the Indian Ocean appear to be closely similar to *Zanclea gemmosa*.*

Two other species of Zanclea are recorded in the literature namely, *Zanclea dichotoma* Mayer (1900) and *Zanclea maasi* Uchida; these have been removed to the separate genera *Zancleopsis* (Hartlaub, 1907) and *Urashimea* (Uchida, 1927) respectively. Weill (1934) has reviewed the systematic position of Zanclea at some length. He has laid stress on whether the nematocyst canals are exumbrellar (" cnidacts " of Günther, 1903) or " endo-ombrellaire "; he gives the name of " cnidothylacies " to the latter. It seems that he has regarded Allman's description (1859) " in the substance of the umbrella " too literally, although Allman states that these are "close upon its outer surface." We are unable to agree with Weill's conclusion that *Zanclea implexa* should be placed in his new genus *Güntherella.*

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* It should be noted that Browne mentions that in one of these the nematocyst capsules on the tentacles were about twice the size of those of *Z. orientalis* (cf. Vanhöffen, 1911).

It is suggested that the synonymy of the hydroid and medusa of *Zanclea implexa* now becomes :

Hydroid. **Zanclea implexa** (Alder).
 ? *Coryne sessilis*,* Gosse (1853).
  Tubularia implexa, Alder (1857).
  Coryne pelagica, Alder (1857).
  Coryne briareus, Allman (1859).
  Coryne margarica, Strethill Wright (1859).
  Coryne implexa, Strethill Wright (1859).
  Halocharis spiralis, Agassiz (1862).
  Zanclea implexa, Allman (1864).
  Gymnocoryne coronata, Hincks (1871).
  Gemmaria implexa, Allman (1872).
  "*Corynitis agassizii*," Murbach (1899).
 ? *Gemmaria gemmosa*, Mayer (1900).
  Zanclea hargitti, Hartlaub (1907).
 ? *Gemmaria costata*, Mayer (1910).
  Gemmaria gemmosa, Stechow (1911).
  Zanclea implexa var. *neapolitana*, Brückner (1914).
  Halocharis gemmosa, Stechow (1923, b).

Medusa. **Zanclea gemmosa** McCrady (1857).
  Coryne implexa, Alder (1862).
  Zanclea implexa, Allman (1864).
  Gemmaria gemmosa, Agassiz (1865).
  Gemmaria implexa, Allman (1872).
  "*Corynitis agassizii*," Hargitt (1905).
  ? *Zanclea costata* (Mayer, 1910 ; Vanhöffen, 1911).
  Güntherella implexa, Weill (1934).

SUMMARY.

A colony of the hydroid *Zanclea implexa* (Alder) has been grown in the laboratory from the first appearance of the polyps until the colony was six months old. A second colony brought into the laboratory in a later stage of development has also been kept alive for six months. Both colonies were growing in association with polyzoa, the second being with *Cellepora avicularis* Hincks. In the earliest stages of development no

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* If future research should show that the *Coryne sessilis* of Gosse is to be regarded as synonymous with *Zanclea implexa* (Alder) then the name *Zanclea implexa* will have to be replaced by *Zanclea sessilis* (Gosse).

perisarc was visible on the hydrocaulus. Medusa bud formation was followed, and some medusæ reared to the adult stage.

A consideration of the changes undergone by the hydroid and medusa during their course of development indicates the necessity of uniting *Zanclea implexa* of the European coasts with *Gemmaria gemmosa* of the American coasts. On the grounds of priority the name for the hydroid must be *Zanclea implexa* (Alder) and that for the medusa *Zanclea gemmosa* McCrady. The medusa with four tentacles, *Zanclea costata* Gegenbaur, is provisionally kept as a separate species.

The genus *Zanclea* is reviewed, and as complete a bibliography as possible has been appended.

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ADDENDUM.

Since passing the final proofs we have seen a report on the Hydroids of the Philippine Islands by Charles W. Hargitt (1924, Philipp. Journ. Sci., Vol. 24, No. 4, pp. 467–505). A new genus and species of hydroid is described, *Zancloidea philippina*. The hydroid differs from Zanclea in possessing filiform as well as capitate tentacles and the medusa in the absence of exumbrellar nematocyst channels. Hargitt mentions a medusa designated as *Zanclea implexa* by Neppi (Adriatische Hydromedusen, Kais. Akad. Wiss. Wien, Vol. 121, 1912, p. 11) which had four tentacles, abaxial purple-red ocelli on the tentacle bulbs, and lacked exumbrellar nematocyst channels. We have ourselves not seen this paper.

On the First Stage of the Medusa *Eucheilota clausa* (Hincks) [= *E. hartlaubi* Russell].

By

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Naturalist at the Plymouth Laboratory.

With 3 Figures in the Text.

In the last number of this Journal (Russell, 1936) I described under the name *Eucheilota hartlaubi* the adult and various stages of a medusa that is fairly common in the Plymouth plankton but had up till then remained undescribed. This medusa was identified with an unnamed medusa which Hartlaub had figured as having been reared from the hydroid *Lovénella clausa* Lovén.

On March 10th, 1936, some *Lovénella clausa* kept in this laboratory by Mr. W. J. Rees liberated medusæ. Mr. Rees kindly handed these over to me so that I could follow the early development. When first liberated the medusa was conically bell-shaped (Fig. 1) and there were scattered nematocysts on the exumbrella. There were two fully developed opposite perradial tentacles, and two non-tentacular perradial bulbs. Rudiments of spiral cirri were developing on either side of the tentacular bulbs. There were four interradial marginal cirri each of which was situated on the umbrella margin about midway between the tentacular and non-tentacular bulbs. On the tentacle sides of each of these marginal cirri was a marginal vesicle with a single concretion. The medusa was 0·75 mm. high by 0·75 mm. broad. The colour of the tentacular and non-tentacular bulbs and the stomach was pale straw. By the next day the umbrella had assumed a more oval bell-shape and the colour of the bulbs and stomach was now a bright orange-yellow. On March 12th the medusa was now 0·9 mm. high and the rudiments of cirri were developing on one side of each non-tentacular bulb (Fig. 2).

On March 14th two of the interradial marginal cirri had disappeared in one specimen. On the 15th another had lost two cirri, and one had lost all four; on March 16th three specimens had lost all four marginal cirri (Fig. 3). The medusæ were not reared further but it was obvious that the next stage would be the development of tentacles on the two non-tentacular bulbs to produce a medusa with four tentacles similar to that in Figure 1 of my last paper (1936).

When I described the medusa *Eucheilota hartlaubi* a small paper written by Hincks (1871) three years after his 1868 monograph had escaped my notice. In this paper Hincks describes and figures the gonotheca and newly liberated medusa of *Lovénella clausa.* His description of the medusa is similar to that just described, except that he makes no mention of any cirri developing at the sides of the tentacular bulbs. Possibly his medusa was liberated at a slightly earlier stage. The marginal vesicles also are drawn by Hincks as being on the non-tentacular sides of the interradial marginal cirri.

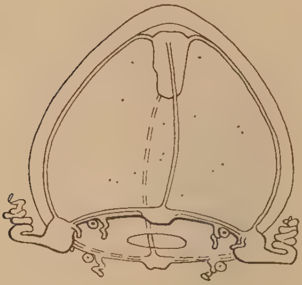

FIG. 1.

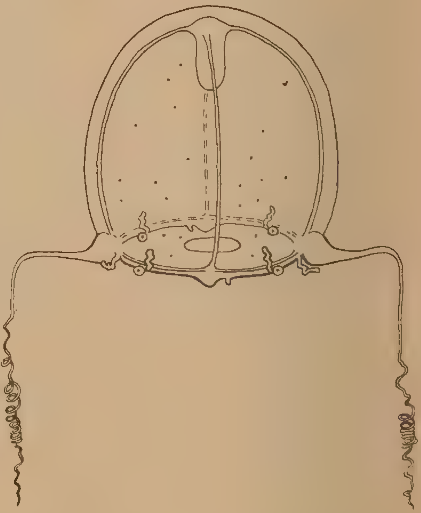

FIG. 2.

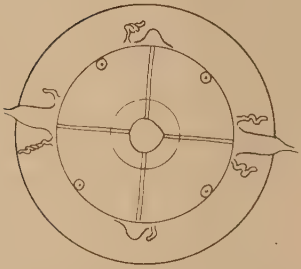

FIG. 3.

FIG. 1.—Newly liberated medusa, *Eucheilota clausa*, 0·75 mm. high by 0·75 mm. broad; Plymouth, 10.iii.36.

FIG. 2.—*Eucheilota clausa* two days after liberation; Plymouth, 12.iii.36.

FIG. 3.—*Eucheilota clausa* seen from below after the four interradial marginal cirri had been lost; semi-diagrammatic; Plymouth, 15.iii.36.

Since Hincks described and figured this first stage of the medusa under the name of the hydroid *Lovénella clausa*, the specific name *hartlaubi* can no longer be kept, and the species must be known as *Eucheilota clausa* (Hincks).

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On a New Species of Hydroid, *Staurocoryne filiformis*, with a Revision of the Genus *Staurocoryne* Rotch, 1872.

By

W. J. Rees,

Research Assistant at the Plymouth Laboratory.

With 11 Figures in the Text.

The writer has recently reared a species of hydroid at Plymouth, which, in the vegetative state, might easily be confused with *Stauridium productum* Wright, 1858. The original creeping stolon from which the colony developed was found on a piece of dead *Eunicella verrucosa* (Pallas) dredged by the S.S. *Salpa* near Stoke Point on March 9th, 1936.

When isolated in a finger-bowl with " outside " sea water the stolon bore no polyps and showed no sign of activity, but three weeks later a single polyp had developed (Fig. 3). From its close resemblance to the figures given by Hartlaub (1895) for *S. productum*, it was at first assumed to be this species and was carefully watched and fed in the hope of rearing the medusæ from it. After a period of time, however, when the colony had increased considerably in size, styloid gonophores were developed.

The type of growth of the fully grown colony is shown in Figures 1 and 2. The stems are elongated and slender, bearing polyps at intervals. Polyps are borne at the summit and also on branches of the main stems. These branches usually arise from one side only of the main stems and it is probable that under natural conditions in the sea these main stems are really stolons. It is also likely that in nature the intervals between the polyps are fairly short. The whole colony has a faint yellow-brown colour which becomes reddish-brown in the polyps and the upper part cf the hydrocaulus. A thin but firm perisarc covers the stolons and the stems almost to the base of the polyps. The perisarc may exhibit faint annulations, but is only distinctly annulated just above the origins of branches.

The initial polyp (Fig. 3) had a trimerous symmetry while the secondary polyps developed later had a tetramerous symmetry. When first observed the initial polyp measured 1·5 mm. from the mouth to the level of the five filiform tentacles and a few days later it had reached full size with twenty-one capitate tentacles in seven alternating whorls of three and measured 2 mm. in length.

Secondary fully grown polyps measure 3·0–3·5 mm. in length from the mouth to the level of the filiform tentacles, and possess 28–36 capitate tentacles in seven to nine whorls of four in addition to the whorl of five filiform tentacles. The tentacles of a whorl are almost always, but not invariably, disposed in the form of a cross. An occasional polyp may exhibit irregularity in the arrangement of the capitate tentacles (Fig. 5). In some polyps each opposite pair of a whorl may not be exactly in the same plane. The filiform tentacles are never quite so well developed as in the initial polyp. They are sometimes rudimentary, or even reduced to mere vestiges (Figs. 4 and 5). The growth of a secondary polyp may be traced in Figures 6–8.

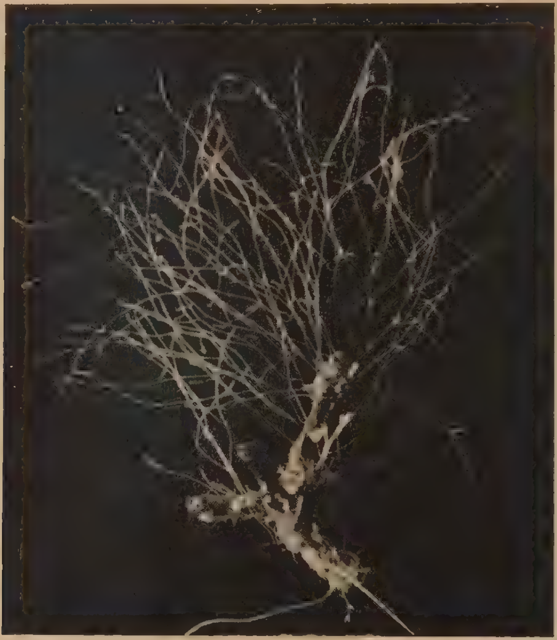


Photo. *E. Ford.*

FIG. 1.—*Staurocoryne filiformis* n. sp. Photograph of the colony, natural size, Plymouth, 3.vi.36.

The gonophores originate in the axils of the capitate tentacles (Figs. 2 and 9) near the middle of the body. When present they usually occur in the axils of the tentacles of the fourth whorl from the posterior end. Only a few polyps developed gonophores and then usually only one. Polyps with two and three gonophores were rare.

The gonophores were first observed as small rounded swellings and had grown to 0·18 mm. in diameter before they could be recognised as styloid gonophores. At this stage there were a very large number of eggs around a well-developed spadix (Fig. 10). The base of the latter at this stage was reddish-brown while the rest of the gonophore including the eggs had a light yellowish-green tinge. In six days it was almost fully grown and had reached the stage shown in Figure 11. It was now 0·35 mm. in diameter and contained much fewer eggs. These were large with prominent nuclei. The whole spadix was now reddish-brown in colour. No male gonophores were observed.

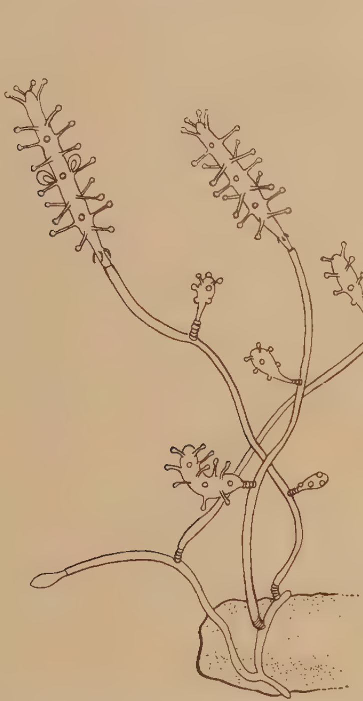
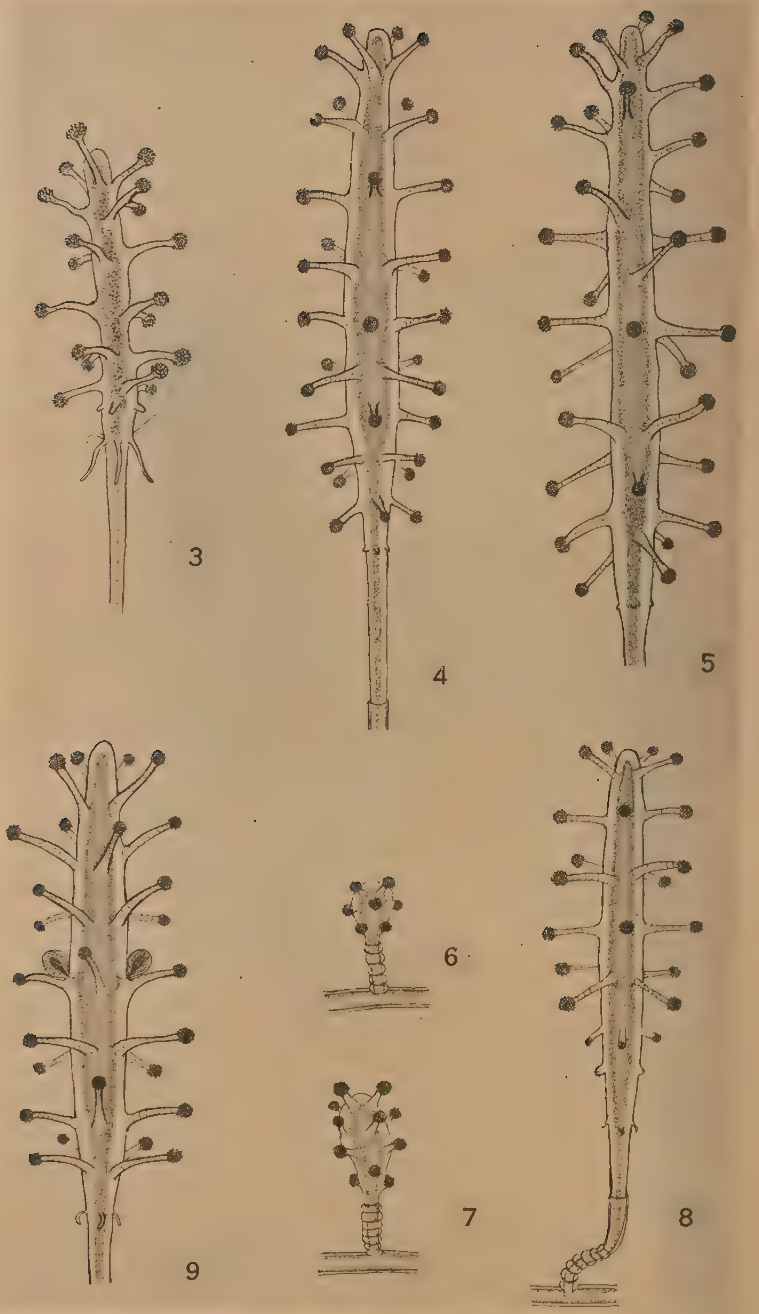


Fig. 2.—*Staurocoryne filiformis* n. sp. A small portion of the colony, Plymouth, 3.vi.36.

The diary of the growth of the colony may be of interest and is given below.

Diary :

9.iii.36	A piece of dead *Eunicella verrucosa* (Pallas) bearing stolons was isolated in a finger bowl.
27.iii.36	Initial polyp observed (Fig. 3).
28.iii.36 *et seq.*	Fed daily on Copepods and Balanus nauplii.
1.iv.36	Buds of secondary polyps appear.
3–8.iv.36	Development of a secondary polyp traced (Figs. 6–8).

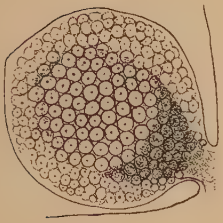


FIGS. 3–9.—*Staurocoryne filiformis* n. sp. Plymouth. 3, The initial polyp, 27.iii.36; 4, A fully developed secondary polyp, 29.v.36; 5, Secondary polyp showing a somewhat irregular disposition of its tentacles, i.v.36; 6, Young secondary polyp, 3.iv.36; 7, Older secondary polyp, 5.iv.36; 8, Almost fully grown secondary polyp, 8.iv.36; 9, Secondary polyp with ♀ gonophores, 29.v.36.

1.v.36	Filiform tentacles of secondary polyps observed to be much smaller than those of the initial polyp (Figs. 4 and 5).
11.v 36	Buds appear on three separate polyps.
12·v.36	Buds recognised as styloid gonophores (Fig. 10).
18.v.36	Gonophores almost fully grown, 0·35 mm. in diameter (Fig. 9).
3.vi.36	Photograph taken (Fig. 1).

The species may be distinguished from *Stauridium productum* in the vegetative state by its greater number of whorls of capitate tentacles and by not possessing more than four tentacles in a whorl. According to Hartlaub, *S. productum* may have five and sometimes six tentacles in a whorl.

It shows, however, a close resemblance to *Staurocoryne wortleyi* Rotch, 1872, in the cross-like disposition of its capitate tentacles. But it differs from this in having a whorl of filiform tentacles. Nothing is known of the gonosome of *S. wortleyi*.



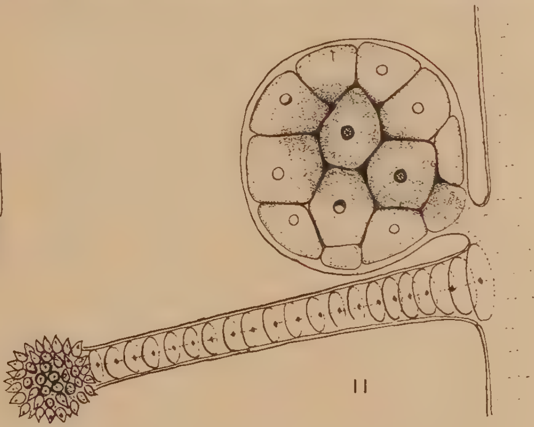


Fig. 10.—*Staurocoryne filiformis* n. sp. Young ♀ gonophore, Plymouth, 12.v.36.
Fig 11.—*Staurocoryne filiformis* n. sp. Older ♀ gonophore, Plymouth, 18.v.36.

As the species reared in the laboratory so closely resembles *S. wortleyi*, it is proposed provisionally to include it in the genus *Staurocoryne* rather than cause confusion by introducing a new genus. It is therefore necessary to redefine the genus *Staurocoryne* to include this new species. The modifications introduced, and the reasons for their introduction, will be discussed at the end of this paper. For the sake of completeness the original description of the genus by Rotch is included below.

The Genus Staurocoryne.

The genus *Staurocoryne* was established by Rotch in 1872 for a new species of hydroid which he called *S. wortleyi*. Rotch defined the genus as follows :—

> "*Gen. char.* Stem simple, rooted by a creeping filiform stolon, the whole invested by a polypary. Polypites terminal, clavate, with several verticils of capitate tentacles disposed in the form of a cross."

and he gives the following description of his species :—

> "Stem simple, of extreme tenuity ; polypary hyaline and smooth ; polypites clavate with 12 tentacles [when fully grown] disposed in 3 whorls of four tentacles each, gonophores not known."

Rotch gives no figure but states that his species nearly resembles Stauridium in the cross-like disposition of the tentacles and Cladonema in its slender mode of growth.

In 1866 van Beneden described a very similar hydroid which he called *Syncoryna Lovenii*.* The tentacles of this species are in whorls of four and number about twenty. Filiform tentacles are not mentioned and the gonosome is unknown.

Another species which might be confused with the present species is *Coryne pintneri* Schneider, 1897. It has been placed in the genus *Stauridium* by Stechow, 1923, although the gonosome is unknown.

Table I gives a synopsis of the characters of these species.

TABLE I.

Species.	No. of whorls of Capitate tentacles.	No. of Filiform tentacles.	Reproduction.	Perisarc.	Habit.	Locality.
Staurocoryne filiformis n.sp.	7–9	5	Styloid gonophores	Distinctly annulated only above the origins of branches	Branched on *Eunicella verrucosa*	Stoke Point Plymouth
Staurocoryne wortleyi Rotch	3	Not mentioned	Unknown	—	Single stems from a stolon. In an aquarium	British (In an aquarium)
Syncoryna Lovenii van Beneden	4–5	Not mentioned	Unknown	—	Branched on shells	Belgian coast
Coryne pintneri Schneider	4	4	Unknown	Distinctly annulated perisarc	,,	Rovigno Mediterranean

Although neither Rotch nor van Beneden mentions the presence of filiform tentacles in their species, this apparent difference is not sufficient to necessitate the creation of a new genus for my species. It is quite possible that filiform tentacles were present in a vestigial condition but on account of this were not observed as tentacles. In all three species the arrangement of the capitate tentacles is similar, but what may be a more important difference than the apparent absence of filiform tentacles, is the much smaller number of tentacles in *S. wortleyi* and in *Syncoryna Lovenii* van Beneden. In this respect *S. wortleyi* and *Syncoryna Lovenii* van Beneden are very similar and may prove to be identical. In the absence of knowledge of their gonosome these two species are provisionally referred to the genus *Staurocoryne*.

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* This must not be confused with *S. Lovenii* Sars which is a true *Syncoryne*.

The following new definition is proposed to include the three species, *Staurocoryne filiformis* n. sp., *S. wortleyi*, Rotch, 1872, and *Staurocoryne Lovenii* (van Beneden, 1866).

Gen. char. Stem simple or branched, rooted by a creeping filiform stolon, the whole invested by a polypary; polypites clavate or subcylindrical borne laterally and at the summits of the stems, with several whorls of four capitate tentacles, usually arranged in the form of a cross; with a single whorl of filiform tentacles or traces of them. Gonophores (sporosacs) borne on the body of the polyp.

The new species *Staurocoryne filiformis* may be characterised as follows:

Staurocoryne filiformis n. sp. (Figs. 1–11). Stem slender elongated and branched, strongly annulated above the origins of branches and faintly in other parts; polypites (when fully grown) with 28–36 capitate tentacles disposed in seven to nine alternating whorls of four tentacles and with a whorl of five filiform tentacles which may be very rudimentary (and even absent in some polyps). Gonophores styloid borne in the axils of the capitate tentacles.

The difference in symmetry between the initial polyp and the secondary polyps is of interest. This phenomenon has been observed in a species of Stauridium by Drzewina and Bohn (1916). The initial polyp in their species had a tetramerous symmetry while the secondary polyps developed later were trimerous. They assumed that this was due entirely to the conditions (laboratory conditions) under which the secondary polyps developed. A study of other hydroids under laboratory conditions, however, shows that although the type of growth and branching may be affected, the polyp itself is nearly always constant in the number and arrangement of its tentacles. It is possible that the initial polyp may prove to be more primitive than the secondary polyps and may be of importance in indicating relationships.

In 1853 Gosse described a juvenile form, *Coryne cerberus*, with three capitate tentacles and five filiform tentacles and this may prove to be the larval form of *Staurocoryne filiformis*, a stage which I missed as the polyp had advanced beyond this stage when it was first observed. A new genus, *Perinema* has been proposed by Stechow (1923) for *C. cerberus*.

Beyond the original description by Gosse, nothing is known of this larval form and the retention of the name *Perinema cerberus* (Gosse) as suggested by Stechow would only create confusion.

There are many records of *Stauridium productum* since the days of Wright and Hincks and these are far too numerous to include here, but in a large proportion of these the hydroid was in the vegetative condition and it is quite possible that some of these at least were not *S. productum* but referable to the present species. It is because of this perhaps that *Staurocoryne filiformis* has not hitherto been recognised as a distinct species.

I am indebted to Mr. E. T. Browne and to Mr. F. S. Russell for much help and advice and to Mr. E. Ford for a photograph of the colony.

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Rearing Animals in Captivity for the Study of Trematode Life Histories.

I. *Larus ridibundus* L., the Black-headed Gull.

By

Miriam Rothschild.

INTRODUCTION.

A TROUBLESOME problem arises in connexion with the tracing of Trematode life histories; namely how to obtain the intermediate and final hosts free from Helminth infections. It was discovered—fortunately early—during the study of the parasites of *Peringia ulvæ* Pennant 1777, that all the species of certain groups of cercariæ, and also related species from other molluscan hosts, encyst most readily in the same species of fish or crab. It is therefore not surprising if the mature trematodes are also to be found in the same host. It is obvious that the greatest confusion can arise from these facts. To add to the difficulty it is often impossible to distinguish between the worms within the cyst, and therefore the dissecting out of cysts for feeding purposes is impracticable.

By far the most satisfactory results are obtained by rearing the hosts in the Laboratory, but unfortunately with marine organisms this is often impossible.

The Black-headed Gull was selected as the final host in a series of experiments, approximately 40 Helminth parasites having been recovered from this bird in Europe. Attempts were made to rear the bird in captivity.

Two dozen eggs were first placed under various hens, but all those were lost owing to the great fragility of the shells. The birds invariably smashed the eggs in turning them. An incubator was then tried but a large series of failures also occurred before the discovery of the correct temperature. Subsequently half the birds died on account of wrong treatment after hatching.

SUCCESSFUL EXPERIMENT.

The eggs, which varied greatly in size, were collected immediately after they were laid and dispatched by rail. They were placed in the incubator (The Curfew Electric Incubator) approximately 14 hours later. The incubator was raised to a temperature of 101–102° F. (38° C.) and maintained at this heat until after the birds were removed to the brooder.

The humidity was about the same as that usually employed for the artificial incubation of ducks' eggs. The upper troughs were filled with sea water.

The following table gives the daily treatment of the eggs :

1st day	(May 22nd)	Set eggs. Closed incubator.	
2nd ,,		Eggs not touched.	
3rd ,,		,, turned twice daily.	
4th ,,		,, ,, ,, ,,	
5th ,,		,, ,, ,, ,,	
6th ,,		,, ,, ,, ,,	
7th ,,		,, ,, ,, ,,	
8th ,,		,, ,, ,, ,,	and cooled for 5 mins. at night.
9th ,,		,, ,, ,, ,,	,, ,, 8 ,, ,,
10th ,,		,, ,, ,, ,,	,, ,, 10 ,, ,,
11th ,,		,, ,, ,, ,,	,, ,, 12 ,, ,,
12th ,,		,, ,, ,, ,,	,, ,, 14 ,, ,,
13th ,,		,, ,, ,, ,,	,, ,, 15 ,, ,,
14th ,,		,, ,, ,, ,,	,, ,, 15 ,, ,,
15th ,,		,, ,, ,, ,,	,, ,, 16 ,, ,,
16th ,,		,, ,, ,, ,,	,, ,, 18 ,, ,,
17th ,,		,, ,, ,, ,,	,, ,, 20 ,, ,,
18th ,,		,, ,, ,, ,,	,, ,, 20 ,, ,,
19th ,,		,, ,, ,, ,,	,, ,, 14 ,, ,,
20th ,,		,, turned. Cooled 1 minute.	
21st ,,		,, not touched. Cooled 1 minute (hatching begins).	
22nd ,,		,, ,, ,, ,, 1 ,,	
23rd ,,		,, ,, ,, ,, 1 ,,	
24th ,,	(June 14th)	(hatching over).	

Hatching took place between the 20th and 24th day. It was noted that the small eggs failed to develop. Without exception the birds experienced difficulty in liberating themselves from the shell and many died in the process. At this stage the mortality was 50 per cent.

After the chicks hatched they were removed to the cooling chamber, but not permitted to move about in it. Activity immediately after hatching had proved fatal in several cases. They were fed approximately seven hours later while still within the cooling chamber. Ten hours later they were removed to the brooder (Curfew Electric Brooder) which was heated to 90° F. (32° C.) and from then onwards fed every 20–30 minutes. The temperature of the brooder was gradually lowered to 70° F. (21° C.) and on the third day the chicks were allowed to run freely in a pen at room temperature.

Care was taken to avoid accidental infection through the food supply. In the case of the final host it is usual to declare an animal free from Helminth parasites if routine examination of the fæces reveals no sign of eggs. Yet it has been shewn repeatedly that many trematode parasites can be present, especially in animals used in the laboratory, and yet no eggs appear in the fæces.

By feeding with boiled food and regulating the supply of vitamins with patent preparations it was hoped to reduce the risk of accidental infection to a minimum. Throughout these experiments it was assumed that water from the hot taps (in London) was free from viable helminth parasites.

Although fish does not appear to be one of the principal components of the food of the Black-headed Gull in nature, it formed the major portion of the diet supplied to these birds in captivity.

The fish was mixed with breadcrumbs, cooked with water or milk, and passed through a sieve until it formed a semi-liquid gruel. This was given with a pipette. De Vons' insect food, thoroughly baked, was added to the food on the third day, the birds pecking at it themselves from off a dish on the floor. In addition to the patent vitamin preparations, a pinch of calcium lactate was added to the diet from time to time.

ACKNOWLEDGEMENTS.

My very best thanks are due to Miss E. Meyerhof for the great trouble she took in rearing the young birds, and to Mr. James Campbell and Mr. Thomas Jeffryes (Leadenhall Market) for supplying me with eggs.

The Ecological Relations between the Herring and the Plankton investigated with the Plankton Indicator.

Part I *by* **A. C. Hardy.**
Part II *by* **C. E. Lucas.**
Part III *by* **G. T. D. Henderson.**
Part IV *by* **G. T. D. Henderson, C. E. Lucas, and J. H. Fraser.**

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Part I. The Object, Plan and Methods of the Investigation.

By
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Professor of Zoology and Oceanography, University College, Hull.

With 10 Figures in the Text.

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INTRODUCTION.

A NUMBER of naturalists have expressed their belief that the movements of the adult herring (*Clupea harengus* L.) at certain seasons are governed by the relative abundance or scarcity of their food or other organisms in the plankton.

Goodsir (1843) wrote that the herring follow the swarms of Entomostraca from place to place. Brook (1886) described how the Loch Fyne herrings enter the Loch when the copepod *Calanus finmarchicus* (Günn.) becomes abundant and remain feeding until the copepods have decreased ; Calderwood (1895), also for Loch Fyne, described opaque yellow belts of Calanus and stated that fishermen told him that beneath such belts closely packed shoals of herring were usually to be met with. Hensen (1886) correlated the occurrence of herrings in parts of the Baltic with the density of copepods. Paulsen (1906) in his study of *Calanus finmarchicus* in Icelandic waters shows that its distribution is most irregular and correlated with it the appearance of shoals of herring. Herdman and Riddell (1913) write as follows : " It seems not unlikely that there is a definite connection between oceanic water containing Calanus in quantity and shoals of herring in the Hebrides. We have noticed on several occasions that we obtained large hauls of Calanus at spots where either the night before or the night after good catches of herring were reported."

Pearcey (1885), who accompanied a herring drifter to the Shetland fisheries, observed that whenever the nets were shot in water rich in phytoplankton (Rhizosolenia) the catch of herrings was small. Fishermen have long considered what they call " weedy " or " stinking " water to be unfavourable for fishing. Bullen (1908) had shown that more mackerel were taken where zooplankton predominated and fewer in water where phytoplankton predominated.

The present investigations form a continuation of the researches into the relation of the herring to its animate environment begun by one of the authors when on the staff of the Ministry of Agriculture and Fisheries in 1922. After making a study of the food and feeding habits of the herring (Hardy, 1924) he wrote : " A second aim of the work is to attempt to establish whether the belief . . . that the movements of the herring are in certain seasons influenced by the occurrence of certain plankton organisms is really a fact or not. If it can be shown to be the case, it should be of the greatest importance to the herring industry."

Preliminary experiments were begun in 1922 and 1923 with a torpedo-shaped instrument called the Plankton Indicator. This first model has already been fully described (Hardy, 1926). Essentially it consisted of a cylindrical tube towed through the water and taken below the surface by means of a weight. Towards the tail end the cylinder was hinged to open and allow a gauze disc (60 meshes to the inch) to be inserted for the collection of the plankton. Its construction and working were kept as simple as possible to enable it to be used readily by fishermen for sampling the plankton at the place where they fished, so that the quantity and kind of plankton could later be correlated with the number of herring caught. The method of preserving and returning the discs was the same as that to be described in the present experiments with the improved Indicator. It was hoped that if marked correlations were established between the catches of herring and different kinds of plankton the instrument could be used as an aid to fishing. The fisherman, having learnt to distinguish the differences in the appearance of the discs, would, by frequently sampling the water, be guided away from unprofitable water and into that in which he would be more likely to catch fish.

Only very limited trials were made with this instrument before the author joined the *Discovery* Expedition and the work was for the time being suspended. As far as it went the experiment showed that in the spring and autumn green or pale green discs due to Phæocystis or diatoms appeared to indicate water in which fishing was likely to be poor. No definite correlation between the zooplankton and the catches of herring could be made out. It was found however that this type of Indicator, taken below the surface by a weight only, was inefficient, and probably did not reach a sufficient depth to sample the plankton in the region of the herring nets. On his return from the Antarctic and appointment to the University College of Hull he planned (Hardy, 1930) a continuation of the experiment with an improved type of Indicator fitted with diving planes to take it to the required depth. The work was planned to be carried out in both the Scottish and English fisheries as a prelude to a wider scheme of charting the plankton of the North Sea in relation to the fisheries month by month by means of continuous plankton recorders operating on steamship lines. In the summer of 1930 preliminary experiments were begun with the Indicator in Scottish waters and in the following year the Council of the College generously equipped laboratories and provided funds, supported by a grant from H.M. Treasury on the recommendation of the Development Commissioners, and from other bodies (see p. 174), to carry the general plan into effect. Dr. G. T. D. Henderson and Mr. C. E. Lucas, specially appointed under the scheme, took up the analysis and working up of the Plankton Indicator material, the former being mainly responsible for the Scottish material and the latter for the English. The present account of the planning, scope and methods of the investigation forms an introduction to their results which follow in Parts II, III and IV.

Description of the Improved Plankton Indicator.

The new Indicator is considerably smaller than that described in 1926, being only 22 inches in length and 3½ inches in diameter with ends tapering to openings of 1½ inches diameter. It is essentially the same as the former instrument except that it is fitted with a system of vanes and weights which make it dive below the surface to the required depth when towed. The construction of the instrument is shown in Figs. 1, 2, 3 and 4. Figs. 1–3 and the following detailed description (slightly modified) are taken from the British Patent specification No. 369715.* The reference numbers in *italics* refer to the numbering in the figures.

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* The instrument is patented in Great Britain and a number of other countries and marketed for commercial use by Messrs. V. D. Ltd., 54 Victoria Street, London, S.W.1, the inventor's royalties on commercial sales being devoted to further research for the benefit of the industry. Investigators who wish to use the instrument for purposes of research may obtain it from Messrs. V. D. Ltd., at a specially reduced rate.

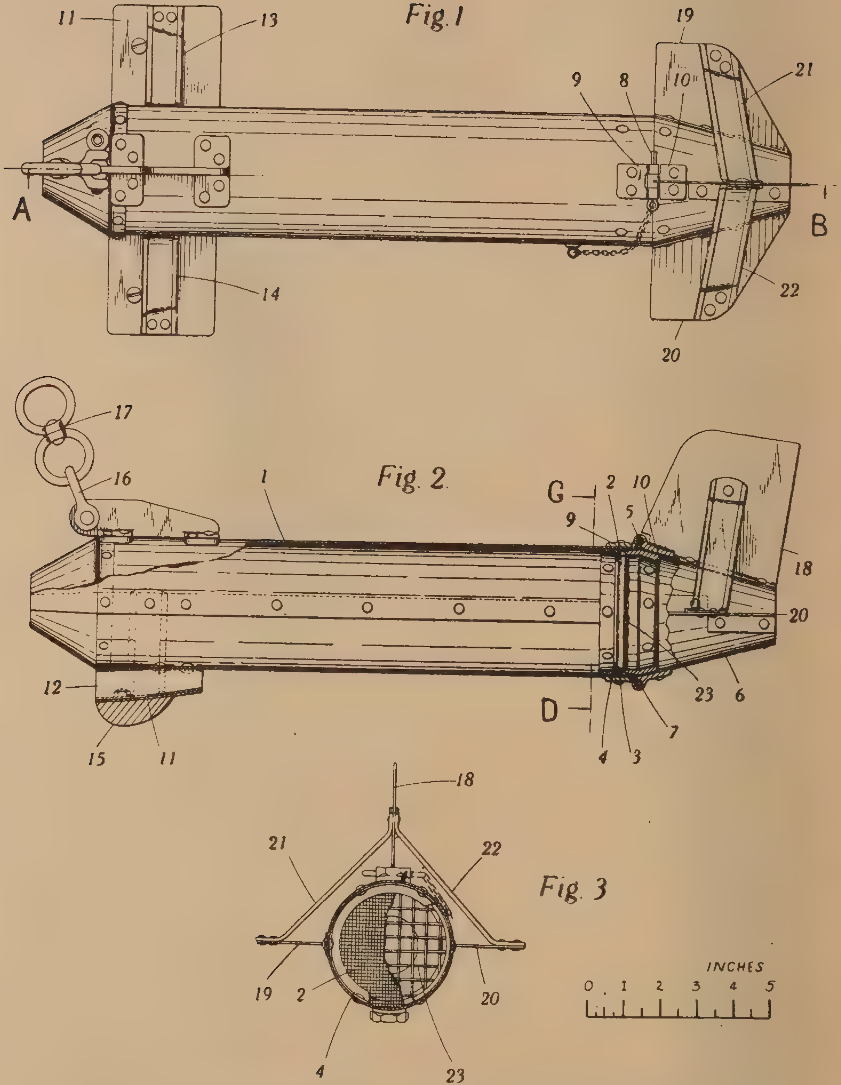
Fig. 1
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Fig. 2
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Figs. 1, 2 and 3.—Showing respectively a plan, a longitudinal and a transverse optical section of the Plankton Indicator. For detailed description and references to letters and numbers see text.

Fig. 1 shows a plan of the instrument. Fig. 2 is a section on the line AB in Fig. 1, and Fig. 3 is a section on the line CD in Fig. 2. It consists of a cylindrical body *1* through the bore of which the water passes as the instrument is towed. A disc *2* of silk gauze* sewn onto a ring† is placed across the bore, the ring abutting against an inwardly projecting flange *4* and being held in position by an annular part *5*. This part *5* is fixed in the tail *6* of the instrument which is hinged at *7* to the cylindrical body *1* so that it can be swung downwards to give access to the disc *2*. When the tail *6* is swung upwards it is locked in position by means of a pin *8* which passes through inter-engaging hinge-like members *9* and *10* fixed respectively on the cylindrical body *1* and tail *6*. The annular part *5* carries cross wires *23* which give support to the disc *2*. The cylindrical body *1* is provided with ends tapering to apertures (1½ inches diameter) smaller than the bore of the cylinder, so that the volume of water entering and leaving the instrument is approximately the same as that passing through the disc of fine mesh gauze. The cylindrical body, 3½ inches diameter, is 16 inches long; the tapering fore end and the tail are 2 inches and 4 inches long respectively.

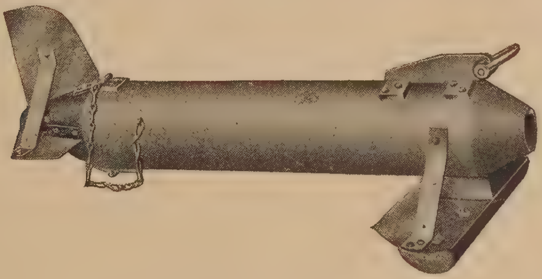

Fig. 4.—The Plankton Indicator.

At its forward end the instrument is provided with a vane *11* (9½ inches by 3½ inches) made horizontal at the front and curving slightly upwards towards the rear; this vane is fixed to the cylindrical body *1* by three struts *12*, *13* and *14* and has on its underside a lead weight *15* (4¼ lb.). On the top of the instrument a shackle *16* and swivel connection *17* are provided for the attachment of the towing line.

The tail is provided with a vertical fin *18* (hind edge 4 inches) and two lateral fins *19* and *20* (the leading edge of each being 2 inches), these being connected to the vertical fin by the bracing members *21* and *22* respectively.

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* In the present experiment quadruple strength Swiss silk gauze of 60 meshes to the inch.

† For research purposes it may be convenient to mount the gauze between two concentric rings which fit tightly one inside the other (as the rings used for holding fabric for embroidery); thus numbers of circles of gauze may be used consecutively, being taken out and preserved in tubes of formalin.

The body and vanes are made of No. 19 gauge galvanized iron. It is important that the vanes should be strong enough to withstand rough usage without being easily bent, but yet not so rigid that they cannot be bent by strong pressure of the hands to make any necessary adjustments to rectify balance.

A much smaller instrument essentially similar to the standard Indicator but only 13 inches long and 1 inch diameter was designed for phytoplankton only ; this was used first in the autumn East Anglian fishery in 1934 and is described in Part IV.

THE CATCHING POWER OF THE NEW INDICATOR.

The new Indicator was purposely made smaller than the original model to facilitate handling on commercial vessels. Whilst a larger instrument giving a larger sample would be preferable for work carried out from a research ship, it was considered highly desirable in the present experiment to reduce the instrument to the smallest size which would yet collect a reasonable sample of zooplankton. Gardiner (1933), using this instrument for a study of the vertical migration and distribution of *Calanus finmarchicus* in the Shields area, suggests that its chief disadvantage as a research instrument " probably lies in the small size of the mouth, the diameter of which is only 3·8 cm. and the number of individuals captured even in a twenty-minute haul may be very small." This is true if it is regarded as an instrument for general research, but designed for this particular research of indicating regions of comparatively dense plankton it is shown to give reasonable samples. As many as 8000 Calanus have been taken in a one-mile tow, whilst the highest number of Limacina (juv. and adult) was close on 100,000. In Table I are shown the analyses of six samples selected to show its catching power of different organisms, each sample representing approximately a mile tow. The largest number recorded for each organism during the course of the experiment is also shown. The average number of Calanus per disc taken in the Scottish and Shields fisheries 1931–1933 were 367 and 382 respectively.

The silk of 60 meshes to the inch was chosen as suitable to yield sufficient numbers of zooplankton including Calanus, and in addition to retain the larger phytoplankton forms when abundant. If a much wider mesh had been used the phytoplankton, even when dense in the sea, would be largely lost, and if a much finer mesh had been used, then the gauze would become clogged with only a medium concentration of phytoplankton, so that the denser zones, which it is desirable to locate, would be less easily distinguished. A finer mesh too, apart from clogging, would, by reduced filtration, diminish the quantity of the zooplankton obtained.

TABLE I.

Showing the Analyses of Six Indicator Samples, each the Result of approximately 1 Mile Tow, and the Highest Number of a Selection of Organisms recorded in such Samples, to illustrate the Catching Power of the Indicator. See p. 152.

Date: Area:	May 31 1931 West Irish.	July 2 1931 East Scottish.	May 23 1932 Shields.	June 14 1932 Shields.	June 27 1932 Shields.	Aug. 19 1932 Shields.	Maximum number recorded.
Phytoplankton (selection only)							
Rhizosolenia styliformis		8,000	1,800				28,500
Rhizosolenia stolterfothii		184,000					184,000
Biddulphia sinensis							19,250
Chætoceros spp.		4,000	21,300				31,200†
Peridiniales		1,000				1,300	9,000
Dinophysis spp.						2,000	30,000
Ceratium spp.		22,800	10,200	900	2,400	112,700	300,000
Zooplankton (selection only).							
Medusæ						1	24
Sagitta spp.			17	2	13	11	1,000
Polychæt larvæ							20,400
Tomopteris							8
Podon			4	8			1,250
Evadne spp.		64		120	40		4,000
Calanus finmarchicus	240	40	270	1,176	400	41	8,000
Paracalanus parvus and *Pseudocalanus elongatus*	1,480		100	96	304	448	2,176
Centropages hamatus and *typicus*	32	110	12		256	56	1,360
Temora longicornis	16	90	32	56	304	16	3,750
Acartia spp.		10	24	56	144	168	4,200
Oithona spp.	120	10	108	104	88	32	1,160
Total Copepoda	1,888	280	550	1,496	1,576	762	11,000
Amphipoda					1		18
Euphausiacea	24						24
Decapod larvæ							195
*Limacina retroversa**	57,000			32		544	96,600
Lamellibranch larvæ		12	4			64	2,700
Cyphonautes larvæ		80	12				750
Actinotrochus larvæ							44
Echinoderm larvæ							1,460
Oikopleura			8	32	16		104
Fish eggs	1				6		128
Fish larvæ and post larvæ					12		12

* See footnote, p. 179.

† Omitting *Ch. socialis*.

It is of interest to note that the mesh used, 60 meshes to the inch, has openings corresponding approximately to those between the gill rakers of the herring. This was only discovered after the choice had been made.

Naturally the small size of the instrument and consequent small quantity of water filtered will prevent a fair sample of the larger and rarer animals being taken. It is possible that by their agility they may be able to escape this smaller instrument; but it should be noted that, employing the paravane principle, the towing wire presents no obstruction to the inlet, which being at the streamlined nose of the instrument cuts the undisturbed water cleanly. The towing wire descending at the end of its catenary curve makes a steep angle with the towing head, and so strikes the water well *above* and *behind* the opening. Quite large young fish, even over 2 inches long, have sometimes been caught whilst mysids, euphausians, decapod larvæ and amphipods are often taken.

Sampling Methods and their Validity.

To carry out the experiment we sought and received the kind and generous co-operation of drifter skippers, and the commanders of gunboats of the Mine Sweeping and Fishery Protection Flotilla and cruisers of the Fishery Board for Scotland. The former were requested to use the Indicator as in the earlier experiment immediately before shooting their nets, the latter to take samples with the Indicator alongside drifters actually fishing, and afterwards to ascertain their catches from the port of landing. In addition we received the kind help of officers of the Ministry of Agriculture and Fisheries and of the Fishery Board for Scotland, who in different ports collected and returned to us the tins of used discs from the drifters and issued new ones in their place. An acknowledgement of our indebtedness to all these skippers, officers and authorities is given on p. 174.

Each drifter was provided with an Indicator and a length of line marked at 10 fathoms from the Indicator, and the skipper was requested to tow it for 1 mile by the log or for 8 minutes at 7½ knots, immediately before arrival at the place where the nets were to be shot. When towed thus, with the mark at the water surface, the Indicator would swim at a depth of four to five fathoms. After towing, the disc was taken out and placed plankton side downwards on a square of calico provided, wrapped up and held by two rubber bands. It was now dropped into a galvanized iron storage tin containing formalin. When the nets were hauled and the quantity of fish caught ascertained, the catch of herring together with the name and number of the boat, date, position, time of shooting and hauling nets were entered on a printed label provided.* This label was then folded up and inserted under the rubber bands securing the corresponding plankton disc. In addition the skippers were invited to add notes on any unusual conditions, state of weather, presence of jelly-fish, etc. that might be of interest. These additional notes have proved to be of value; they are analysed and discussed in a separate paper by Mr. Lucas and Dr. Henderson (1936).

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* The style of label was similar to that shown in the first Report on trials with the Indicator (Hardy, 1926).

The herring nets are drifting for many hours and the fish may come into the nets early or late after shooting. The plankton is sampled before the nets are shot. Although the ship and nets are drifting, the water sampled may have moved some distance from the nets before the fish are caught; this distance will usually only be small, but if the plankton is very patchy then the nature of the plankton at the position where the fish are actually caught may differ from that at the position of sampling. Further, the mile length over which the Indicator was towed, whilst ending approximately at the point where the drifter begins shooting, may lie at any angle to the line of nets. Again, although fish may be present in large numbers they may not swim into the nets; the presence or absence of fish in the nets is by no means a certain indication that the fish are abundant or scarce in the vicinity. These factors may tend to obscure correlations, but in spite of this, certain correlations have been established by considering a sufficient number of samples.

Whilst the provision of vanes forcing the Indicator down is a great improvement over the simple weight used in the first experiments, the depth at which it fished cannot be regarded as strictly constant. The same will apply to the duration of tow. However willing the fisherman may be to help the scientist, and they have shown remarkable keenness, it is only to be expected that circumstances may cause some small variation in procedure. If the ten-fathom mark on the line provided was not at the surface, or if the speed of the vessel was considerably greater or less than 7½ knots, then the depth of the Indicator would vary accordingly. It is probable that its depth varied between 7 and 10 metres, more usually nearer the lesser depth, and the duration of tow may have varied to some extent above or below the required 8 minutes or one mile by the log. Since we are usually considering comparisons between wide ranges of plankton values these variations will not seriously affect the results.

The time at which the hauls are taken is of importance on account of the differences in vertical distribution of the zooplankton at different times of the day. The samples taken by drifters were all taken immediately before the shooting of the nets. Whilst the time of shooting varies to some extent, depending partly upon the time required to reach the grounds and upon weather conditions, there are indications that the time of shooting from May onwards becomes later and later until August, when it becomes earlier again. Roughly these average times follow the course of the setting sun through the season, although there appears to be a lag after mid-summer when the sun begins to set earlier. The drifter samples on an average are taken before sunset and bear to one another a reasonably similar relation to light intensity for each area considered.* In the treatment of results only samples from limited areas and limited time periods (usually half-monthly periods) are compared. The differences in the behaviour of organisms, such as Calanus, in regard to vertical distribution in different areas and at different seasons have been shown to be great, as witness the results of Russell (1928), Marshall, Nicholls and Orr (1934, also Nicholls, 1933) and Gardiner (1933) for the Plymouth, Clyde and Shields areas respectively. The bearing of vertical migration upon the commercial application of the Indicator is dealt with on p. 171. The fishery cruisers and naval patrol ships aimed at obtaining the samples as near the time of shooting as possible, but a number of samples have been taken at other times between shooting and hauling. In the Shields area such samples do not form an appreciable proportion of the total, but they are more numerous in the Scottish area.

The spatial distribution of samples in different areas and periods varies considerably. At one time the drifters may be fairly evenly scattered over a wide area, or at other times they may be spread widely but in irregular patterns, or again they may be concentrated in a small patch. Naturally a greater range of variation in plankton values and catches of fish may be expected with a wide distribution than with a confined one; but it does not invariably follow. Whilst as many as twenty Indicators have been issued to drifters or patrol ships at one time, usually not more than four or five have been working simultaneously in any one fishery. The curves showing the average catch of herring for the drifters using the Indicator and those for all the vessels in the same fishery are found to be similar, as will be seen in Mr. Lucas's and Dr. Henderson's papers on the Shields and Scottish results which follow. Thus the herring catches of the drifters using the Indicator can be taken on an average to be fairly representative of the whole fleet. Our main object is to find out whether the variations in the plankton are in any way correlated with the variations in the catch of herrings made by the vessels using the Indicator, and if such correlations are found to exist to see to what extent the Plankton Indicator may be an instrument of commercial value. A by-product of this research is the plankton material available for a general ecological study of the plankton of the area concerned; the value of this material is strictly limited by the factors here discussed, particularly the limitations in depth and time (when vertical migration is considered), and the variations in spatial distribution just referred to. Nevertheless, keeping in mind these limitations, some features of the general ecology of the plankton from the different regions can be discussed in regard to the Scottish and English areas in the papers which follow.

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* In the Southern Bight there is not the same regularity in shooting times, but here in the autumn fishery, where the herring are not feeding, we are only concerned with phytoplankton correlations, the zooplankton being of no importance.

Other factors which may tend to obscure correlations existing between the plankton and catches of herring are the variations in the lengths of 'fleets' of nets used and the duration of fishing. The normal variation in the length of the fleet of nets is from 1 to 1¼ miles, but occasionally extremes of ¾ or 1½ miles may be used (probably these do not occur amongst any of our boats). Since only a few of the boats have supplied us with information regarding the length of the fleet of nets corrections for length have not been made. All the drifters taking part in the experiment were steam and not motor drifters. Whilst the average duration of fishing varies for different boats, the variation in the average catch of these boats bears little or no relation to the time the nets are out, as will be seen in Table II where we are able to compare the average catch of four drifters, termed A, B, C and D* in the Shields fishery over two months in 1932 during which the skippers supplied times of fishing. No doubt if comparison between catch and duration of fishing could be made over very long periods of time some positive correlation must emerge, but, for the shorter periods we are considering, such relations are insignificant because other factors governing the shoaling and swimming of the herring are of much greater importance.

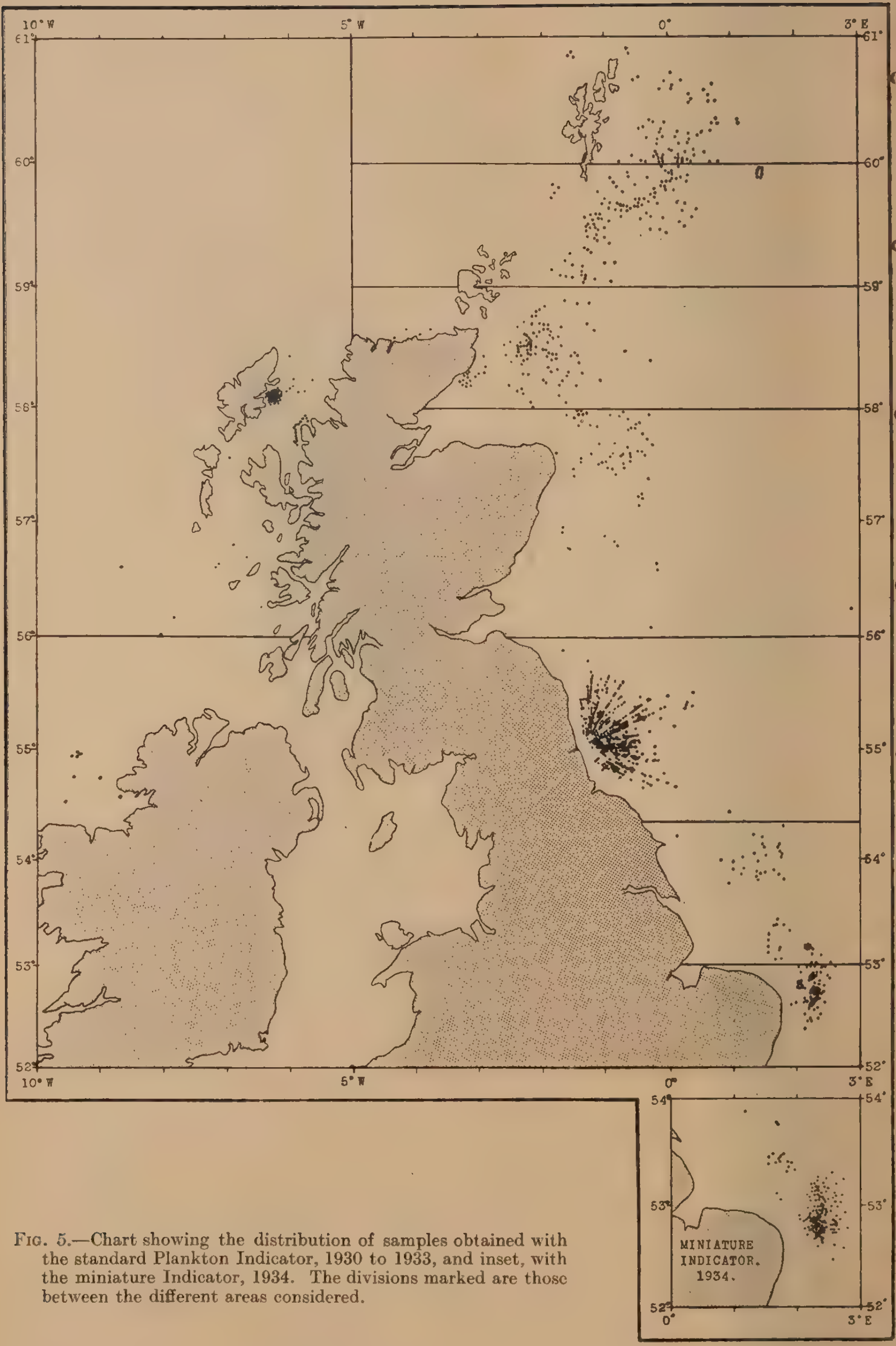
TABLE II.

		Drifter "A"	"B"	"C"	"D"
May 16th–June 15th.	Av. duration of fishing in hours.	4·5	7·6	9·8	10·5
	Av. catch in crans.	*3·0*	*4·2*	*4·0*	*4·1*
June 16th–July 20th.	Av. duration of fishing in hours.	4·1	6·3	10·4	9·0
	Av. catch in crans.	*6·6*	*3·2*	*6·4*	*2·5*

Extent of Material.

During the course of the experiment just over one thousand and four hundred (1406) records of catches of herring with accompanying Indicator samples of plankton were obtained. Of these, 1256 were taken with the

* The drifters are referred to by letters since the owners and skippers of the vessels may not wish their relative catches to be made public.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MINIATURE
INDICATOR.
1934.

Fig. 5.—Chart showing the distribution of samples obtained with the standard Plankton Indicator, 1930 to 1933, and inset, with the miniature Indicator, 1934. The divisions marked are those between the different areas considered.

standard Indicator in the Scottish and English fisheries (with a few in Irish waters) in 1930–33 and 150 with the miniature phytoplankton Indicator used in the East Anglian fishery of 1934. Not all the analyses of the samples with the standard Indicator have been used in the Calanus correlations; some, as explained in the papers which follow, have had to be rejected on account of their isolation in time and space or given only secondary consideration. But all have been useful in relation to the presence or absence of phytoplankton. The general distribution of the samples is indicated in Fig. 5 and in greater detail in the charts in Parts II and III. Altogether forty-three vessels took part in the experiment, of which thirty-five were commercial drifters.

All the samples just referred to and treated in this series of papers are concerned with the drift net fishery. A considerable, not yet sufficient, amount of material has been collected in relation to the practice of herring trawling which is increasing in importance. Here Indicators have been used in the upper layers as well as in a modified form attached to the trawl itself. It is hoped that a paper on their treatment will be published later.

Methods of Analysis and Correlation.

Owing to the pressure of water on the disc during towing and the later pressure whilst wrapped in calico in the storage tins awaiting examination, the samples are seldom in so good a condition as are those from tow-nets. Whilst most species, including all crustacea, are identifiable although damaged, some, such as Oikopleura spp. and the more delicate larval forms, are very much disintegrated and so liable to be missed in analysis.

The samples obtained in 1930 and 1931 were as far as possible analysed for all species, the whole sample being counted if small or sub-sampled if large. On account of the large number of samples and limited time available, it was decided to confine the analysis in subsequent years to those forms for which there appeared to be any indication of correlation in the results of 1930 and 1931. Thus in 1932 and 1933 only the following organisms were estimated: all phytoplankton, the copepod *Calanus finmarchicus*, total Copepoda, the pteropod Limacina, together with records of any of the more unusual forms including fish larvæ and eggs. This restriction of analysis was regrettable but inevitable; the samples, however, have all been preserved, so that if further analysis at a later date appears desirable the material is still available.

The zooplankton correlations with herring catches for 1930 and 1931 appeared to yield two very striking results: a marked negative correlation with the pteropod Limacina and a marked positive correlation with the copepod *Calanus finmarchicus*. Thus for the total 513 observations made in these two years the following table for Limacina can be drawn up:

Number of Limacina on disc.	Number of Observations.	Average catch of herring in crans.*
0	201	13·6
1–99	147	10·9
100–249	38	9·6
250–499	33	9·0
500–999	34	3·6
1,000 and over	60 (59)†	4·6 (2·9)†

This result may be further expressed thus:

With 0–99 Limacina the av. catch is 12·5 crans (348 observations)
,, *100+* ,, ,, ,, ,, ,, *6·3* ,, (*165* ,,)

A similar negative correlation was found in each of the separate subareas, except the East Anglian autumn fishery. A particularly marked falling off in catch was noted when the number of Limacina exceeded 500. For this reason in making the Calanus correlations the examples associated with over 500 Limacina were at first omitted, giving the following result for the Scottish fisheries only:

Number of Calanus on discs.	Number of Observations.	Average catch of herring in crans.
0	18	3·2
1–99	135	5·1
100–249	24	7·3
250–499	16	12·9
500–999	15	14·8
1,000 and over	15	22·0

Again this result may be further expressed thus:

With 0–99 Calanus the av. catch is 4·8 crans (153 observations)
,, *100+* ,, ,, ,, ,, *13·3* ,, (*70* ,,)

or split into the two years

1930

With 0–99 Calanus the av. catch is 5·2 crans (29 observations)
,, *100 +* ,, ,, ,, ,, ,, *28·6* ,, (*23* ,,)

1931

With 0–99 Calanus the av. catch is 3·9 crans (112 observations)
,, *100+* ,, ,, ,, ,, ,, *5·9* ,, (*48* ,,)

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* A cran is a commercial measure of herring by volume. It may be taken on an average to equal approximately 1000 fish, but the numbers may vary considerably for different sizes of fish.

† Excluding a single catch of 102 crans in the autumn East Anglian fishery.

Again in each of the separate Scottish areas* where a reasonable number of trials were made a positive Calanus correlation was found.

Attempts were first made to correlate the total Copepoda with herring catches, and positive correlations were found if we adopted a system of weighting the different species of copepods approximately according to their relative mass (a suggestion by Mr. Lucas similar to that independently developed by Gunther, 1934). But it was found that Calanus, having so great a mass compared with other forms, overweighted all other species together, so that such total copepod correlations were almost equivalent to Calanus correlations.

As the work progressed into 1932 and 1933 it was found that both the ranges of Calanus numbers and the catches of herring varied greatly from area to area and at different times of the year. Let us suppose that A and B are two widely separated fishing areas. Whilst it is found that there is usually a correlation between the higher catches of herring and higher Calanus samples in each fishing area, it does not follow that if the average number of Calanus in fishery A is greater than in fishery B, that the average catch of herring in A will be higher than that in B. Whilst, as we shall see, the movements of the herring within limited areas appear to be correlated with the relative abundance of its food, Calanus, within that area, it does not follow that the ratio of the numbers of herring taken in two separated fisheries will bear a relation to the ratio of the numbers of Calanus in the two fisheries. Again in any one fishery the average number of Calanus may be greater earlier in the season than later on, but it does not always follow that the herring will be more abundant earlier in the season than later and *vice versa*, yet in *any one part* of the season more herring may be found, on an average, where there are more Calanus.

Thus it became necessary to treat the results from different fishing areas separately, and to divide the material collected in each area into short-time periods. The boundaries of the areas (Fig. 5) will be defined in Parts II and III; the time periods chosen were half-months.

As already explained, at first we related the associated catches of herring to the Calanus numbers below and above 100, or to a scale, as shown in the table on p. 160. But it was soon found that in one area the majority of samples might contain more than 100 Calanus whilst in another area (or in the same area at a different time) only a few samples would contain more than 100 Calanus.

A new system of correlation was sought, which would have a closer significance in all areas and in all seasons, and which would enable one the better to weigh up the possible commercial value of the correlations.

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* In the Shields area in 1931 there was a progressive change from a positive correlation to a negative one as the season advanced; this is discussed in Part II.

Each series of samples considered is now arranged in ascending order of Calanus numbers and the series divided into halves ; one half containing all the samples of lower Calanus value and the other half all those of higher Calanus value. The associated catches of herring are also entered in the table. The average catch of herring relating to the two halves is now estimated. Two examples will illustrate the system adopted ; these are shown in Table III and Table IV. If the number of samples in a given series is odd, the catch of herring corresponding with the middle Calanus value is halved and one half shown on each side of the table, as in the example in Table IV.

TABLE III.

CALANUS-HERRING TABLE FOR THE EASTERN SCOTTISH AREA 59°–60° N, JULY 16TH–AUGUST 1ST, 1932.

	Poorer Calanus water.		Richer Calanus water.	
	Calanus. numbers.	Herring in crans.	Calanus numbers.	Herring in crans.
	1	0·0	1420	0·0
	1	24·0	480	19·0
	20	20·0	332	10·75
	25	4·75	330	59·5
	40	0·0	280	63·0
	42	4·5	245	37·5
	68	0·75	204	61·0
	88	72·0	180	9·5
	96	30·0	165	2·0
	101	1·0	125	47·0
	105	0·0	120	36·0
Totals :	587	157·0	3881	345·25
Averages :	53	14·27	353	31·39

Grand total catch : 502·25 crans for 22 landings.

If all the catches had been made in water of the richer Calanus values the expected (theoretical) total catch would have been 690·5 crans, i.e. a theoretical gain of 188·25 crans over the actual total catch obtained when fishing at random. This may be expressed as a (theoretical) gain of 37·5%.

The differences in the ranges of Calanus values and the catches of herring in the examples chosen is seen to be great, illustrating the unsuitability of adopting a uniform scale of Calanus values. The method adopted enables one to compare the commercial value of the instrument in different areas, where the numbers of herring and Calanus differ considerably. These results have been obtained by drifters not using the instrument to find the most suitable water (except where stated in the Shields 1933 season), but simply sampling the state of the plankton where they happened to shoot their nets in the ordinary course of fishing.

TABLE IV.

Calanus-Herring Table for the Shields Fishery, July 1–15, 1933.

	Poorer Calanus water.		Richer Calanus water.	
	Calanus numbers.	Herring in crans.	Calanus numbers.	Herring in crans.
	65	20·0	2800	31·0
	96	16·0	2520	23·0
	140	2·0	2480	12·0
	150	3·0	2000	5·5
	170	35·0	1920	10·0
	355	7·0	1745	1·0
	390	4·0	1440	1·0
	400	15·0	1280	70·0
	565	1·0	1200	3·0
	585	3·0	1120	12·0
	645	39·0	1080	60·0
	800	6·0	810	6·0
	(800 Calanus . . . 6·0 crans half shown on each side)			
	(400)	3·0	(400)	3·0
Totals	4761	154·0	20795	237·5
Averages	$381^{12\frac{1}{2}}$	$12{\cdot}3^{12\frac{1}{2}}$	$1664^{12\frac{1}{2}}$	$19{\cdot}0^{12\frac{1}{2}}$

Grand total catch : 391·5 crans for 25 landings.

If all the catches had been made in water of the richer Calanus values the expected (theoretical) total catch would have been 475 crans, i.e. a theoretical gain of 83·5 crans over the actual total catch obtained when fishing at random. This may be expressed as a (theoretical) gain of 21·3%.

We may suppose that by using the indicator to find water rich in Calanus the drifters could make nearly all their shots in water having a Calanus value at least as high as that which they actually got in the *higher half* of their trials when sampling at random, and sometimes they should be able to get into water of higher Calanus values than any so obtained. In each series we have worked out the theoretically expected catch if all the catches had been in water of higher Calanus value and compared it with the actual total catch, expressing the theoretical gain (or loss in some instances) as a percentage of the actual total catch. These estimated percentage gains (or losses) have been used as a measure of the correlation between the herring and Calanus throughout. Only series containing ten or more samples have been considered when arriving at conclusions regarding correlation. In the Scottish fishery secondary series of six to ten samples are tabulated but used only in general support of primary series results. Owing to the fortuitous nature of the fishing and the often small number of samples in each series taken, the actual percentage gain of any one series by itself is of little significance as a measure of the herring-Calanus correlation; and so the commercial efficiency of the instrument must be based upon a consideration of all the different area-period results in the Scottish fisheries and in the Shields fisheries. Since the conditions differ so widely in the different areas—i.e. the average numbers of herring being caught (and the differences in price of fish in different areas)—the commercial value of the instrument must be measured by taking the *average of the percentage gains or losses.* It appears that under these particular circumstances the averaging of the percentage gains or losses is the only means of obtaining an approximate conception of the commercial value of the instrument. To consider the actual total numbers of herring landed for all the right- and left-hand columns of the tables of the different areas, and estimate the total percentage gain would give a very distorted result, for, as seen, the average number of herrings varies greatly in different areas and also the number of samples in the different series varies widely. The figures for some area-periods would be unduly weighted by the larger number of samples in these area-periods than in others. Further, as already pointed out, in considering the commercial value of the instrument the considerable variation in prices in different areas and seasons is of importance. That the *average of the percentage gains or losses* is a figure of real value as an indication of the efficiency of the indicator is shown in the following way. If, in the Shields fishery where the number of samples per series is larger than in the Scottish fishery, we divide the Calanus values for all series into the lower quarters and the higher three-quarters, and again into the lower three-quarters and higher quarters instead of into lower and higher halves and work out the average of the percentage gains or losses in the same way as for the halves, we get figures which show a regular progressive gain to the fisherman who fished exclusively in water of the higher three-quarters, the higher half, or the higher quarter of Calanus values: this is described by Mr. Lucas on p. 213 in Part II which follows.

In the Shields fishery, in addition to estimating the average gain which may be expected for all boats fishing in the water of higher Calanus values, it has been possible to work out separate estimates for each of the individual drifters taking part in the experiment. Each vessel shows a substantial estimated average gain.

In investigating the Limacina-herring correlations it was also desirable to treat the material in small areas and short-time periods to avoid the overlapping of varying ranges of concentration. In dealing with Limacina in this way the marked negative correlation of 1930 and 1931 indicated on p. 160 was still evident, but at Shields in 1932 this negative correlation was not always maintained, the tendency being towards a positive one although not constant. In 1933 the tendency was again negative. We are thus unable yet to come to a definite conclusion regarding the relation of Limacina to the herring; the matter is discussed in Parts II and III.

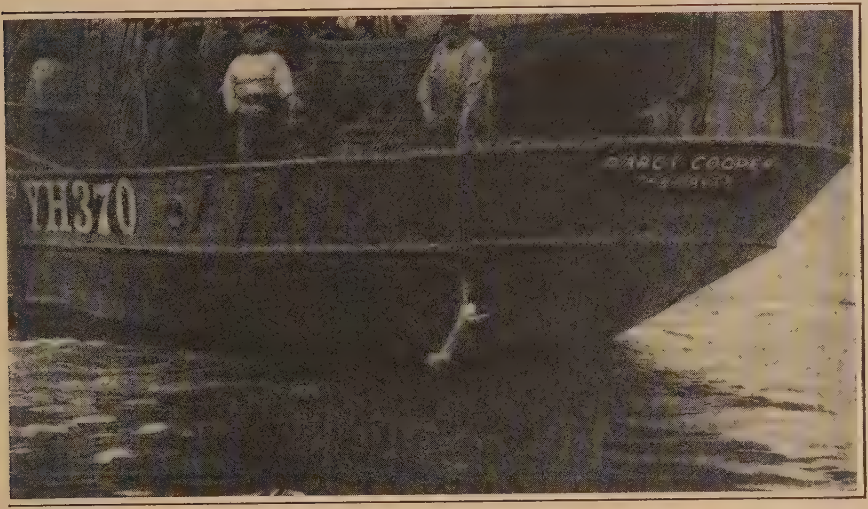


Fig. 6.—The Plankton Indicator in use on a drifter.

The phytoplankton correlations for both Scottish and English waters, including the special survey in the autumn East Anglian fishery of 1934 with the miniature indicator, are dealt with together in Part IV by Dr. Henderson, Mr. Lucas and Mr. Fraser. Here for each area the average catch associated with discs coloured green or greenish brown by phytoplankton is directly compared with the average catch associated with those not so coloured. A marked negative correlation is established.

The Commercial Application of the Indicator.

As a result of the analysis and treatment of the data collected with the Plankton Indicator, described in detail by my colleagues Dr. Henderson, Mr. Lucas and Mr. Fraser in the papers which follow, two important commercial applications of the instrument have been established.

When the Indicator yields a disc coloured green or greenish brown (due to abundance of phytoplankton) the catch of fish to be expected in such water will be low in comparison with that which may be expected in water yielding a disc not so coloured. All the fisherman has to do in applying this principle is to sample the water from time to time with the Indicator as he seeks his fishing position and steam out of any such areas as give a disc which can be seen at a glance to be coloured green or greenish brown.

Fig. 7.—Fishermen examining the Indicator disc for phytoplankton signs.

Fishermen using the indicator commercially are provided with colour charts for reference. Fig. 6 shows an Indicator being used from a drifter and Fig. 7 a disc being examined for coloration. This indication will be particularly valuable in the spring, early summer, and autumn fisheries when dense phytoplankton concentration may be met with. In the great autumn fishery off East Anglia it has been shown to be particularly important and a special miniature Indicator has been designed for use in this area where the zooplankton correlations are not important and where the concentration of the fleet in a small area renders the standard Indicator less easily used. This miniature Indicator is described on p. 283 in Part IV. Reference has already been made to the traditional belief amongst herring fishermen that what they call " weedy " or " stinking " water is bad for fishing and such conditions have been shown to be due to an abundance of phytoplankton (Pearcey, 1885; Bullen, 1908; and Hardy, 1923). Whilst occasionally such water may be detected by the fishermen by a discoloration of the water itself, more usually it is only after they have fished that they can detect it by a slimy feeling and the smell of the nets. In our sampling of the East Anglian fishery in the Autumn of 1934 vessels fished in water giving a green indication on 42 out of 150 occasions. Samples were obtained from October 7th to November 20th; throughout this time there were both areas which did and areas which did not yield green discs; on all but few occasions the catches associated with the former were considerably lower than those associated with the latter. (See Part IV p. 288).

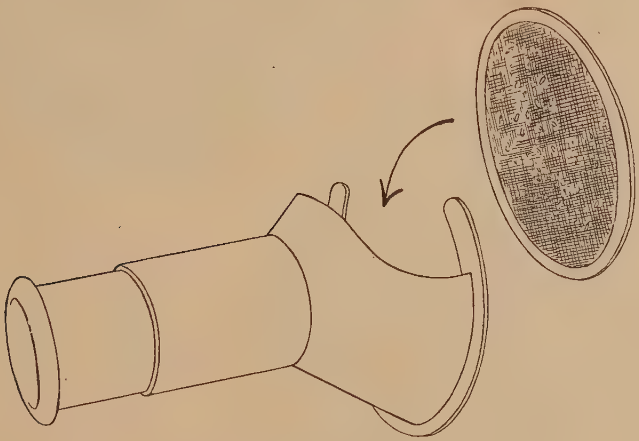


Fig. 8.—The lens holder used for examining the disc for Calanus indications.

The other important commercial result is that concerned with the positive correlation found between the herring and its important food organism, the copepod Calanus, in the summer fisheries in both English and Scottish waters and also confirmed in the Icelandic fisheries by Fridriksson (see p. 173). By avoiding the water which is poorer in Calanus and fishing in that which is the richer in Calanus an average gain in catch of 18·3% over that obtained by fishing at random is estimated for the Scottish and Shields fishery together for all periods 1931–33; or omitting the incomplete 1931 year at Shields: 23·0% The standard errors for the results from the Shields and Scottish fisheries have been calculated and are given in Parts II and III (pp. 209 and 253).

The examples given in Tables III and IV, and in the histograms in Parts II and III will show that herrings are not always taken in larger numbers where there is more Calanus. Good catches may be taken in poor Calanus

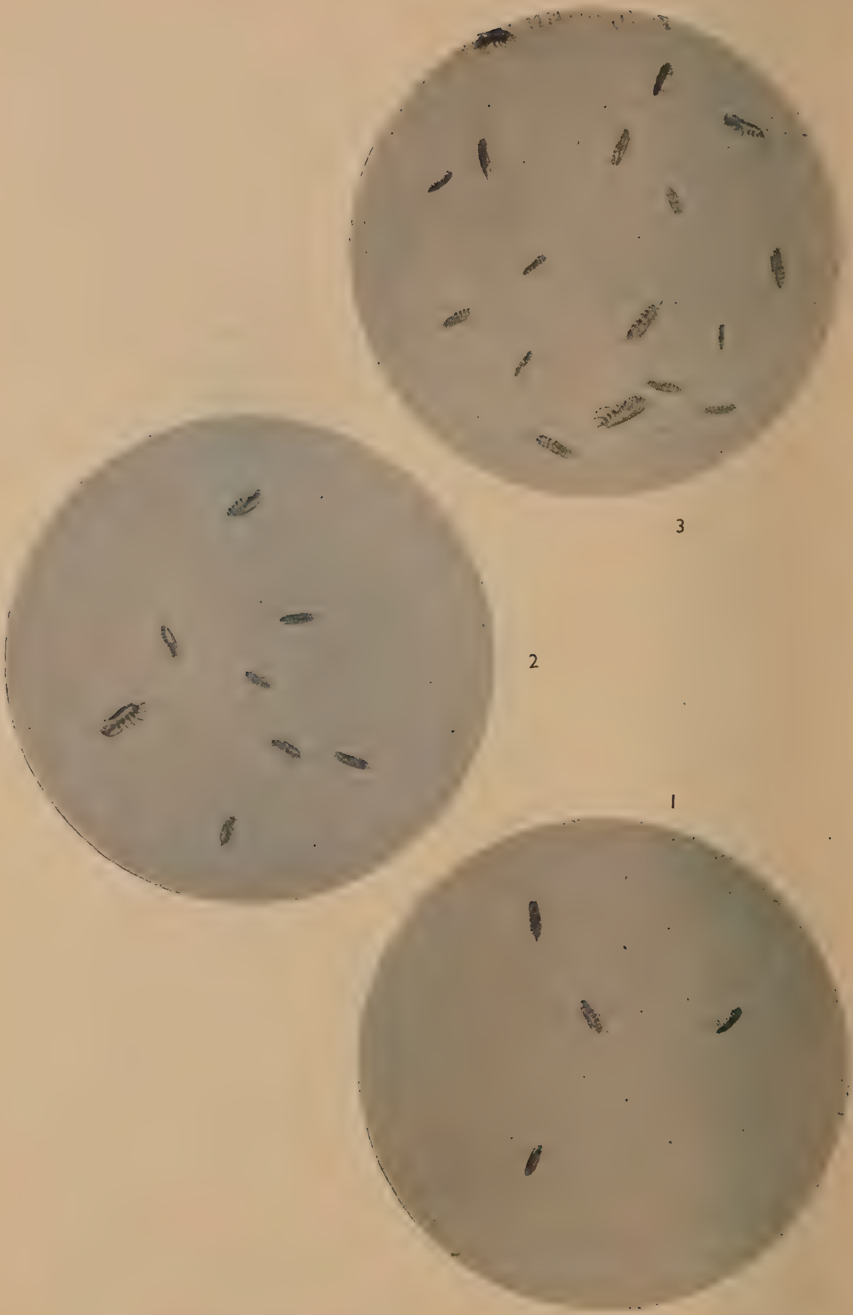
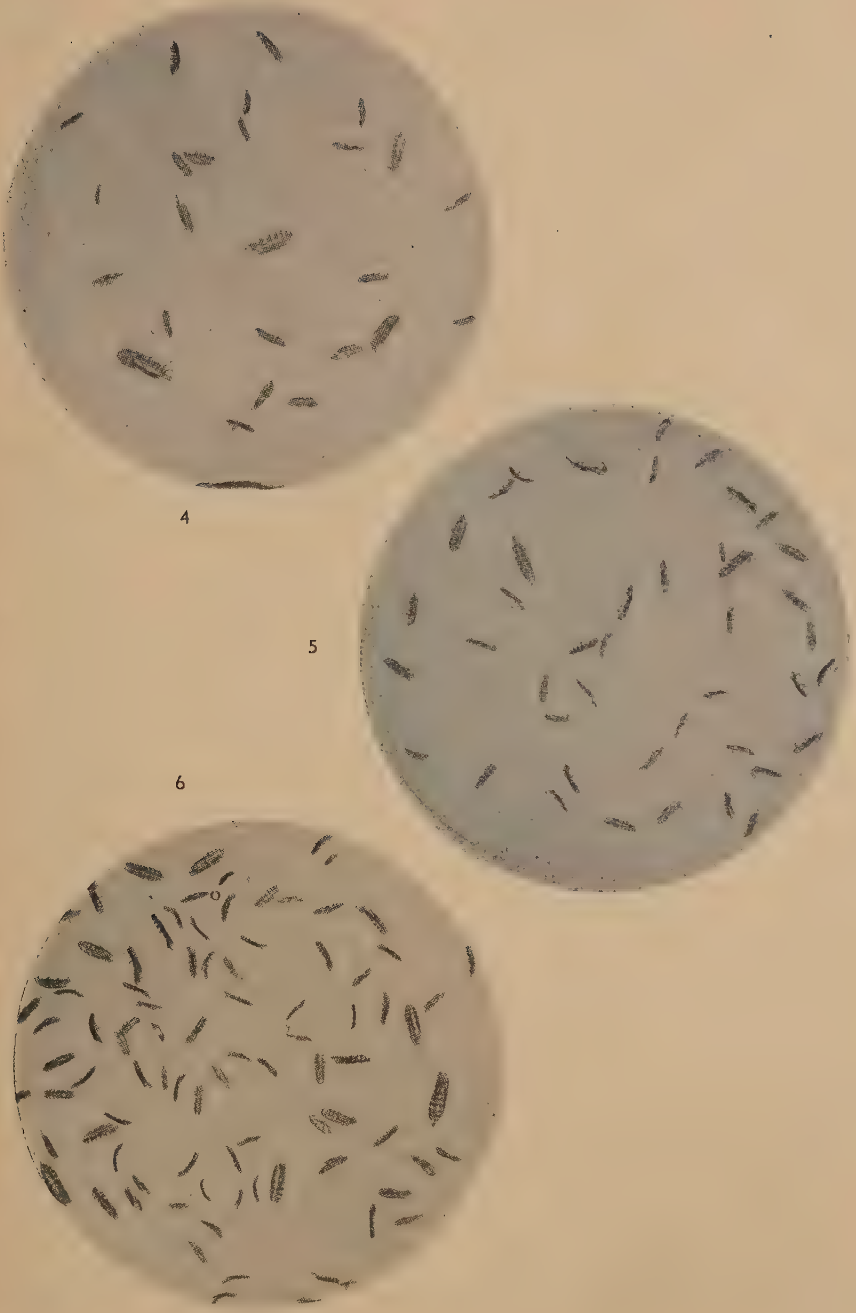


FIG. 9.—Photographic chart, provided with the Indicator for commercial use, showing variations in Calanus numbers as seen on the discs through the examination lens. Photographs by J. H. Fraser.



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5

6

Fig 9.—*contd.*

water and poor catches in rich Calanus water. But if the instrument is used systematically throughout a season to find the richer Calanus water then on an average more herring will be taken than if simply fishing at random. Whilst over some periods a boat may actually lose by following this principle, in the end it should have made a marked gain. For all the individual vessels that have been followed through periods varying from 20 to 156 voyages we have been able to demonstrate that had they fished in the richer Calanus water they should all have got substantial gains.

In planning this work it was first thought that if such positive food correlations were obtained it would be possible to use a simple colour indication, as in the case of the phytoplankton, in that a quantity of copepods on the disc would give it a pinkish tint. In practice it has been found that the colour of Calanus varies very much, sometimes it is almost colourless, and other copepods, not useful as indications, may give a pink coloration. At times too Echinoderm larvæ have been found to colour the discs a brick red. Calanus far exceeds all the other Copepods in size and can readily be recognised through a simple lens. For the commercial application of the Calanus indications, a simple lens holder, Fig. 8, is provided, into which the disc can be dropped and held up to the light. The fishermen are provided with photographic charts showing the appearance of varying numbers of Calanus, Fig. 9, as well as photo-

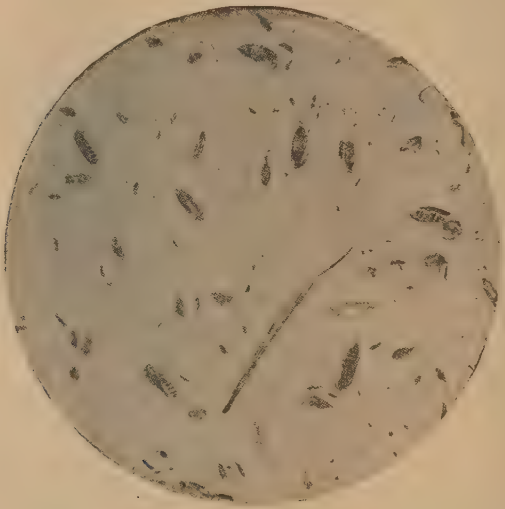

Fig. 10.—Photograph provided with the Indicator for commercial use showing Calanus with other plankton forms as seen on the disc through the examination lens. Photograph by J. H. Fraser.

graphs of Calanus as it might appear on the disc mixed with other plankton, Fig. 10. A sample disc with actual Calanus preserved between sealed sheets of celluloid is also provided for demonstration. The fisherman very soon learns to recognise its form. On steaming out to the fishing grounds he would take a sample with the Indicator every few miles, towing it each time for a mile by the log without stopping the ship. A small hand reel has been designed to be fixed to the side of the ship to make light work of hauling in the Indicator. At each sampling he will take out the disc and examine it in the lens holder. He will note how the Calanus abundance compares with the scale of photographs provided and the position from which the sample was taken. He is supplied with a number of discs (which may be washed and used again) so that he can keep them on one side for reference when he comes to decide on his position for fishing. Thus after taking perhaps six samples over the proposed fishing grounds he will return to fish at the point where the greatest number of Calanus was obtained. As Mr. Lucas shows on p. 214, the skipper who takes more trouble (and uses a little more fuel) in trying to find out the richer Calanus water is likely to gain a higher reward.

We must now consider the possible influence of the diurnal vertical movements of the Calanus on the application of this principle. It is well known that Calanus usually tends to move from the lower to the upper layers of water as darkness approaches. The Indicator is designed so that it swims at a depth of 7 to 10 metres from the surface.* Even at this depth some increase in the number of Calanus may be expected as time advances towards sunset and darkness. If, for example, in the process of searching, the fisherman's samples have yielded in turn moderate Calanus, few Calanus, many, very many, few, moderate and he returned to the position which yielded " very many " this should still be the richest position since it can be expected that at all the positions the Calanus would be increased by a proportional amount through vertical migration. Only in the exceptional circumstance of the Calanus being quite evenly distributed is he likely to experience a gradually increasing quantity of Calanus, through the influence of vertical migration, as he steams over the ground as evening approaches; if this was the case, then such an even distribution of Calanus in itself would nullify the operation of the principle for the herrings might be expected equally at any point. Our results show that such an even distribution of Calanus is hardly ever met with. At times, no doubt, the vertical migration of the Calanus may upset the application of the principle; but we believe they will be rare.

During the summer fishing at Shields in 1933 some of the skippers were actually using the Indicator to find the more profitable positions for fishing. Two of these skippers have published accounts of the working of the instrument and it may be of interest to quote from them since they show exactly how it may be used with advantage.

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* It takes up this position when a mark on the towing line, 10 fathoms from the Indicator, is at the surface of the water.

The following extracts are taken from an account by Mr. Ronald Balls, master of the S.D. *Violet and Rose,* YH 757, in *The Fishing News* of February 24th, 1934.

> "Calanus is very easily recognised on the disc, and any boats that could do most of their fishing in water containing it could certainly expect a considerable increase in their catches. . . .
>
> First of all, it is most important that the Indicator should be used as consistently as possible over at least a whole summer season for a real test of its usefulness, because, although there are cases where when good feed is found an excellent catch results, this is not always the case, and occasionally the opposite happens. It is only by continuous use over a period of weeks that the benefits of the instrument become apparent.
>
> Nevertheless, I have found during the summer that at any time when a small belt of Calanus has been found, with the surrounding waters devoid of feed, a superior catch has always been the result of shooting in the feed. Naturally, one cannot expect this to happen very often, and when Calanus is very widespread choice of position for fishing is unnecessary unless, as sometimes happens, there are also patches of unfavourable plankton about, when the Indicator can be used in its second capacity.
>
> As an illustration of this I can quote from my own experience on Monday, July 10, of last year. On this day, steering north by east from Rattray Point, we found Calanus fairly good from 30 miles onward to 50 miles, but although each disc we towed was seemingly good enough to shoot on, I noticed that every one was clogged with a fine, jelly-like substance. Continuing on our course, at 54 miles we obtained a good disc of Calanus which was also quite free from the jelly; in fact, the remarkable liveliness of the Calanus here was noticeable after their lifeless condition when amongst the jelly on the earlier discs.
>
> Thus, although we had found good feed for over 20 miles, there was also the unfavourable organism present until we were 54 miles from Rattray. We shot exactly where we had towed this good disc, and our catch of 70 crans next morning was well above the average at Peterhead or Fraserburgh.
>
> I have also found that when there is no Calanus about but only wide patches of weedy or unfavourable water, the same procedure of steaming until clean water is found usually has a beneficial result. . . .
>
> From May 1 to July 30 we shot 69 times—40 shots were in water with little or no Calanus, and the average catch for these was 3 crans; 29 shots were in water containing good or fairly good Calanus, and the average for these 29 shots was 9·5 crans. Thus, when Calanus was present there was an increase of 216 per cent in the average catch."

Mr. H. K. George, master of the S.D. *Ocean Spray*, YH 264, also wrote in *The Fishing News* (June 16th, 1934) as follows:

> "I feel sure that other skippers amongst your readers will be interested in hearing of further practical results obtained with the Indicator, as if properly worked and studied it will greatly assist a skipper in finding the best fishing grounds in the spring and summer fishing. As examples I will quote two instances which stand out vividly in my mind.
>
> Herrings were very scarce and dear at Shields on this particular day, and the only boat to have any was the motor boat *Twilight* with 12 crans from N.E. by N. 20 miles, so that was where we started for that day. After we had steamed 8 miles I put the Indicator over and pulled it up every mile until we were 13 miles without seeing the slightest signs of Calanus.
>
> Between 13 and 14 miles there were a few on the disc; from 14 to 15 miles it was a very good disc; from 15 to 16 miles it was only moderate again, and from then on to where the *Twilight* was shooting her nets at 20 miles there was nothing on the disc, so we steamed back to where we found the Calanus, and we found it again.
>
> We shot our nets and got 16 crans of herrings, which was a good night's work, and not one of the other boats got any, they all being three miles and more to the north of us.
>
> The next instance was one day we had 40 crans from 22 miles E.N.E., and steaming

off that day I put the Indicator over and the best disc I got was between 17 and 18 miles, but I carried on the 22 miles and could not find any Calanus, so I steamed back to where I got the good disc and found it again.

The same thing happened as before, and with that and many other instances when it happened it gave me complete confidence, though I don't pretend to think it is infallible, as at times we have found feed and got very few herrings, and at others we have not found any feed and yet we have got a few herrings, though not many.

I also noticed that the week when herrings were plentiful at Shields, the sea where the herrings were was full of Calanus, but it didn't last long in so widespread a nature, neither did the herrings. I have had several chats with other skippers who I know take a great interest in this work, and I am sure we were unanimous on the point that the skipper who has an Indicator and takes interest in it will be streets ahead of them who just trust to pot luck.

Some of the older skippers don't believe in it, though I think in a very short time they will have to admit."

Our experiments in the summer fishery ended in 1933 so that we have no data for the Shields fishery in 1934. This is unfortunate because conditions during the 1934 season at Shields do not appear to have been favourable to the use of the Indicator. Whilst we have no statistical evidence from the analysis of samples, the skippers using the Indicator have told me that they were not able to get the same advantage from it as in the previous year. In the summer of 1935, however, Mr. Balls obtained more samples for us which showed an average gain in the richer Calanus water of 23·4%; the details of these samples are given as a postscript to Part II on p. 240. Some further samples were also obtained from the Scottish fishery in 1935 and the results of these correlations are appended to Part III.

CONFIRMATION OF RESULTS.

The results obtained from the material by Mr. Lucas for the English fisheries and Dr. Henderson for the Scottish fisheries are mutually confirmatory in regard both to the positive Calanus and the negative phytoplankton correlations. A preliminary account of these Calanus results was first published in the *Fish Trades Gazette*, May 12th, 1934, and further confirmation has recently been obtained from Iceland. Mr. Fridriksson of the Fisheries Department at Reykjavik kindly arranged to carry out experiments with the standard Plankton Indicator in relation to the herring in Icelandic waters. He has recently (Fridriksson, 1935) reported on the results of his experiments and the following is quoted from his English summary: ". . . we can clearly see a positive relation between the maximum catches [of herring] and the maximum numbers of *Calanus finmarchicus*. On the other hand we can find no pronounced relation between the catch . . . and the two frequent plankton copepods Acartia and Temora. . . . No relation can be found, neither positive nor negative, between the number of Sagitta and the amount of the catches."

ACKNOWLEDGEMENTS.

In carrying out these researches we have been dependent upon the kind help of a very large number of people. We wished to make the experiment as representative as we could of conditions in the fishery and to this end it was desirable to enlist the co-operation of as many skippers of drifters as possible. At one time and another, for varying periods, thirty-five drifters have taken part and it has been a source of great encouragement to us to know how keenly interested most of the skippers have been in the progress of the work. It is not always easy for the practical fisherman to give the necessary time to such work, especially in the trying conditions of rough weather. We extend to them our warmest thanks and appreciation for this great help and to a number of them for the kind hospitality shown to us when we have accompanied them on their voyages. A list is given below of the skippers who took part in the work.

We are equally indebted to the Commanding Officers of the gunboats of the Mine Sweeping and Fishery Protection Flotilla: H.M.S. *Boyne* (Lieut.-Com. S. A. Brooks, R.N.), H.M.S. *Cherwell* (Lieut.-Com. H. R. Gordon-Cumming, R.N.), H.M.S. *Dee* (1930; Lieut.-Com. W. V. H. Harris, R.N., M.V.O., D.S.C. and Lieut.-Com. C. K. Adam, R.N., 1931–33: Lieut.-Com. S. A. Brooks, R.N. 1933: Lieut.-Com. W. Walmsley, R.N.) and H.M.S. *Foyle* (Lieut.-Com. R. Dalby, R.N.); to the Commander and Officers of the Fishery Cruisers *Minna*, *Norma* and *Freya* belonging to the Fishery Board for Scotland and to the Research Vessel *City of Edinburgh* (Skipper John Munro) of the Department of Scientific and Industrial Research, all of whom have taken numerous samples alongside drifters fishing; to the Fishery Officers and Collectors of the Ministry of Agriculture and Fisheries and the Fishery Board for Scotland, who have rendered us every assistance at the different ports in the collection of Indicator discs and data; to the Humber Pilot Steam Cutter Co. Ltd. for allowing us to carry out tests with instruments on their ships and to members of the firm of Messrs. Bloomfield's Ltd. who have given us special facilities both in the placing of instruments on their drifters and providing working accommodation at Lerwick and Yarmouth. To all these gentlemen we extend our most grateful thanks.

We are also most grateful to Professor R. A. Fisher, F.R.S., for kindly examining the methods used in making the correlations and for suggesting the working out of the Standard Errors given in Parts II, III and IV.

This investigation has been made possible by grants from the College and the Treasury on the recommendation of the Development Commissioners, and in addition the Leverhulme Trustees, the Hull Fishing

Vessel Owners Association and the Fishmonger's Company have contributed funds to the development of the wider, but associated, plankton survey by means of recorders.

The Council of the Royal Society has graciously made a grant of £80 towards the cost of publishing the results.

Masters and their Steam Drifters taking part in the experiment.

F. E. Aldred : *Territorial LT 339.*
L. Balls : *Emulate YH 349, Ocean Retriever YH 307.*
R. Balls : *Violet and Rose YH 757, Golden Spray YH 97.*
D. Brown : *Ocean Crest YH 876.*
E. Brown : *Ocean Rambler YH 725.*
R. Brown : *D'Arcy Cooper YH 370.*
E. G. Catchpole : *Repay LT 273.*
L. Claxton : *Tessie YH 769.*
J. Condon : *Ocean Vim YH 88.*
S. Corey : *Ocean Trust YH 160.*
A Cowie : *Poseidon BCK 157.*
S. Cumby : *Ocean Guide YH 24.*
A. Dawkins : *Ocean Pilot YH 325.*
L. Dawkins : *Ocean Sunlight YH 28.*
N. Garrod : *Effort LT 1043.*
H. K. George : *Ocean Spray YH 264.*
J. C. George : *Golden Gain YH 91.*
J. George : *Ocean Treasure YH 574.*
L. George : *Ocean Pioneer YH 189, Ocean Reward YH 730, Ocean Toiler YH 312.*
B. Hall : *Ocean Crest YH 876.*
B. Haylett : *Ocean Gain YH 184, Ocean Treasure YH 574.*
A. Larner : *Hilda Cooper YH 392.*
J. Lawn : *Ocean Dawn YH 47.*
J. More : *Mayberry WK 79.*
R. W. Nunn : *Ocean Lux YH 84.*
S. Roper : *Ocean Pioneer YH 189.*
A. Sago : *Boy Alan LT 331*
P. H. Smith : *Ocean Trust YH 160.*
R. C. Stubbs : *New Spray YH 135, Togo YH 248.*
— Tungate : *Emulate YH 349.*
— Turrell : *Girl Margaret LT 420.*
K. Thompson : *Ocean Lifebuoy YH 29.*

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Part II. Zooplankton-herring Correlations in the English Fisheries.

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With 24 Figures in the Text.

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INTRODUCTION.

THE English fisheries which were investigated with the Plankton Indicator in 1931, 1932, and 1933 were divided into three areas, i.e., those off Shields, the Humber mouth and the East Anglian coast (this last fishery was also sampled in 1930). All the samples in the Shields area lie between 56° 00′ N. Lat. and 54° 20′ N. Lat., whilst the majority (80%) lie in the area between 54° 45′ N. Lat., and 55° 30′ N. Lat. and a line parallel to and some 40 miles from the coast. This is an area of some 1600 square miles. In the Southern Bight Lat. 53° 00′ N. was taken as a division between the Humber and the East Anglian areas. The distribution of all the samples is shown in Figs. 1 to 4. With the exception of the samples obtained by the Ministry of Fisheries research ship *Onaway* in June, 1931, and four samples obtained by H.M.S. *Cherwell* in September, 1933, all those in the Shields area have been collected by individual drifters engaged in the fishery. The Humber and East Anglian samples were obtained from both drifters and gunboats of the Fishery Protection and Mine Sweeping Flotilla alongside drifters fishing. The manner of collecting these samples has been described in Part I (p. 153).

The greater part of this work refers to the ecological relations of the herring to the copepod *Calanus finmarchicus** (Günn.) and to the pteropod *Limacina retroversa*† (Flemming).

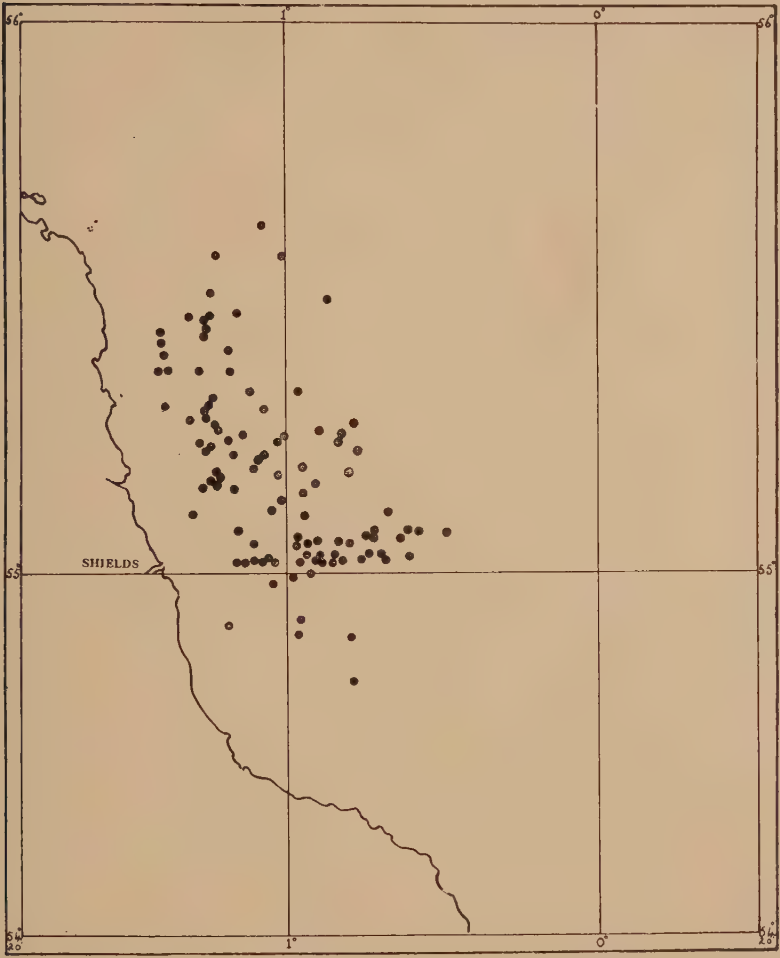

Fig. 1.—Showing the distribution of the Indicator samples in the Shields fishery in 1931 (29th June to 8th September).

In the first two years of the Scottish work (1930 and 1931) and the first year at Shields (1931) complete analyses of the plankton samples were made. Little sign of correlation between the herring and zooplankton forms other than Calanus and Limacina could be detected. Originally attempts were made to correlate the herring catches with total copepoda,

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* Throughout this paper the term Calanus is used to imply *Calanus finmarchicus* (Günn.).

† No other species have been identified, but at times differences in form have been noticed and it is possible that occasionally other species of the genus have been included in the general term Limacina used throughout the paper.

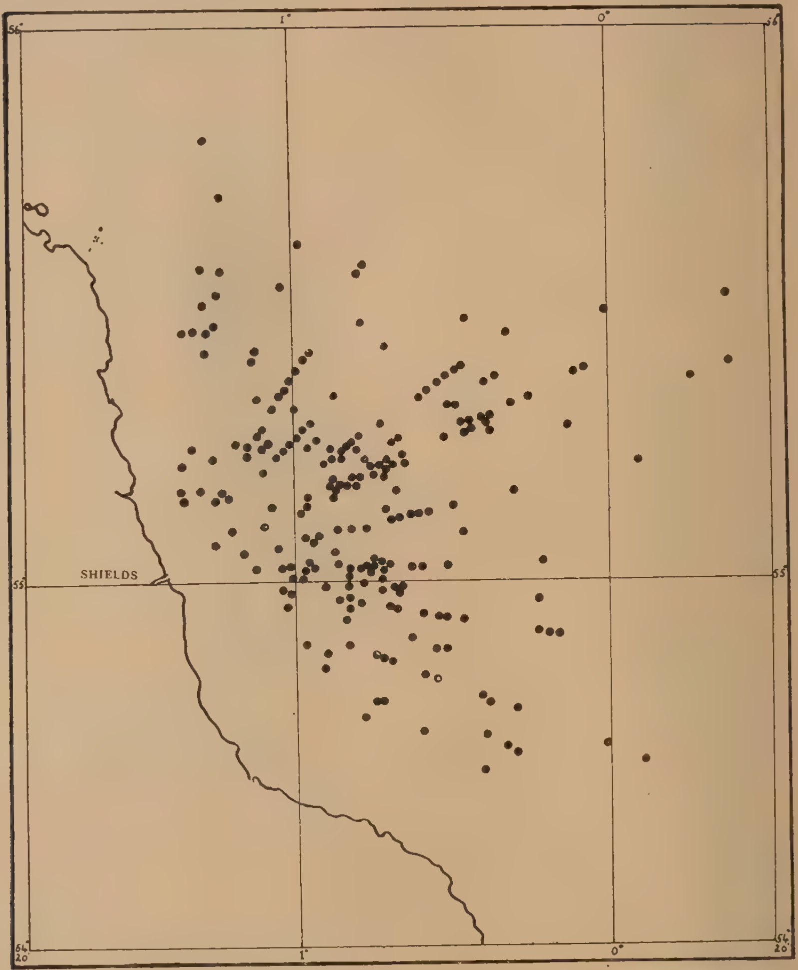

Fig. 2.—Showing the distribution of the Indicator samples in the Shields fishery in 1932 (3rd May to 14th September) Excluding one catch with position doubtful.

and positive correlations were found if we adopted a system of weighting the different species of copepoda approximately according to their relative mass. But it was then found that Calanus, having so great a mass compared with the other forms, overweighted these together to such an extent that total copepod correlations were usually almost equivalent to Calanus correlations. In 1932 and 1933 the analyses were restricted to Calanus, total Copepoda, Limacina and the phytoplankton as described

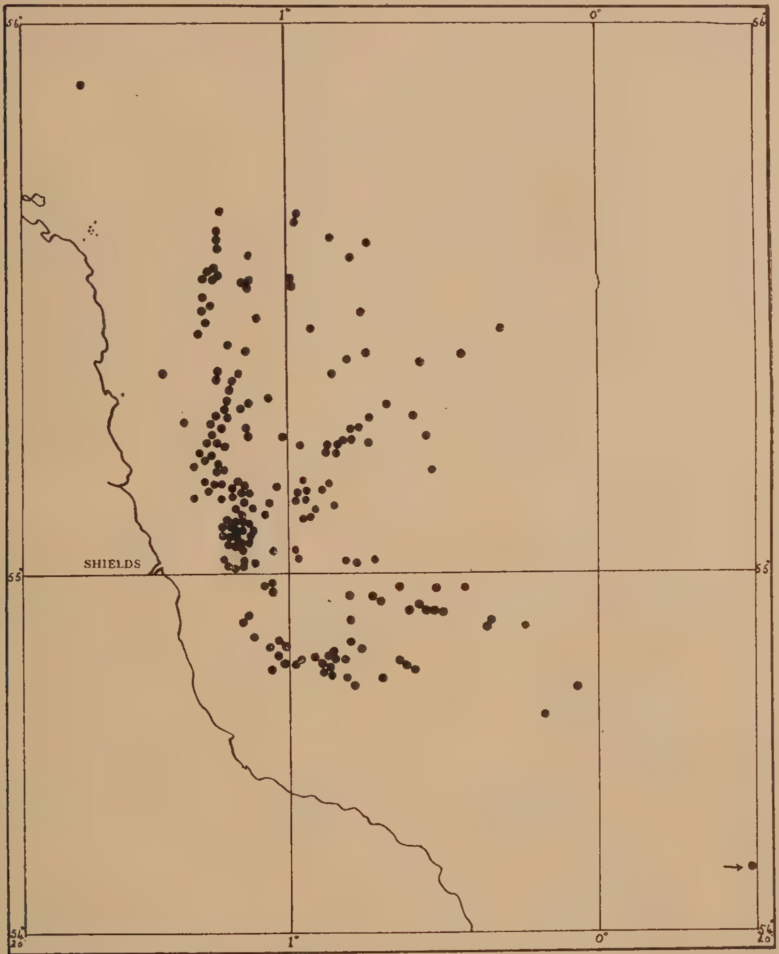

Fig. 3.—Showing the distribution of the Indicator samples in the Shields fishery in 1933 (1st May to 1st September).

on p. 159 of Part I. Fridriksson (1935) using the standard Indicator in Icelandic waters found, as far as his experiments went, no correlation with zooplankton other than Calanus (as quoted on p. 173 of Part I).

TABLE I.

SUMMARY OF DATA RELATING TO THE CALANUS-HERRING CORRELATIONS BASED ON THE RESULTS OF ALL DRIFTERS USING THE INDICATOR IN THE SHIELDS FISHERIES IN 1931, 1932 AND 1933.

Period and Year.	No. of Samples.	Calanus range.	Average Calanus.	Herring range in crans.	Average Herring in crans.	Calanus-herring Correlations.				
						Total No. of herring in crans corresponding to lower and higher Calanus values.		Average No. of herring in crans corresponding to lower and higher Calanus values.		Percentage Increase or Decrease of the catch on the "higher" side compared with the catch of the whole series.
						Lower.	Higher.	Lower.	Higher.	
1931.										
June	30	12–350	87	0·8–60·0	12·8	165·8	218·0	11·1	14·5	+13·6
29 June/15 July*	21	0–216	64	1·0–70·0	18·0	207·5	170·8	19·8	16·3	− 9·7
16–31 July	37	0–625	76	1·0–59·0	19·1	458·1	247·2	24·8	13·4	−29·9
1/15 Aug.	17	0–260	93	1·0–47·0	11·8	141·0	60·0	16·6	7·1	−40·3
16 Aug./8 Sept.*	29	0–280	68	0·0–30·0	8·2	115·5	123·0	8·0	8·5	+ 3·1
Totals 1931	134	0–625		0·0–70·0		1087·9	819·0	80·3	59·8	
1932.										
1–15 May	16	0–900	197	0·0–10·3	2·2	4·4	30·8	0·6	3·8	+75·1
16/31 May	43	0–2150	474	0·0–17·0	3·5	43·6	106·0	2·0	4·9	+41·7
1–15 June	50	45–3215	864	0·0–17·0	4·1	98·8	107·8	4·0	4·3	+ 4·4
16/30 June	45	0–3350	912	0·0–16·0	4·4	94·5	104·0	4·2	4·6	+ 4·8
1–20 July*	32	0–545	189	0·0–21·0	4·9	63·0	95·0	3·9	5·9	+20·3
1–15 Aug.	11	0–1045	175	1·5–40·0	10·5	82·8	32·5	15·1	5·9	−43·6
16–31 Aug.	17	0–550	121	0·1–16·0	4·7	25·9	54·0	3·0	6·4	+35·3
Totals 1932	214	0–3350		0·0–40·0		413·0	530·1	32·8	35·8	
1933.										
1–15 May	12	10–1360	647	0·5–15·0	6·3	33·5	42·5	5·6	7·1	+11·8
16–31 May	11	2–525	170	0·5–13·0	6·0	26·5	39·0	4·8	7·1	+19·1
1–15 June	40	0–2200	200	0·0–13·0	2·1	34·6	48·0	1·7	2·4	+16·2
16–30 June	38	0–1800	389	0·0–41·0	8·6	183·0	142·0	9·6	7·5	−12·6
1–15 July	25	65–2800	1022	1·0–70·0	15·7	154·0	237·5	12·3	19·0	+21·3
16/31 July	25	0–4340	648	0·0–65·0	13·2	92·5	237·5	7·4	19·0	+43·9
1–15 Aug.	28	0–325	71	0·0–56·0	7·8	65·4	151·6	4·7	10·8	+39·7
16 Aug./1 Sept.*	11	0–205	67	0·0–5·0	1·0	3·1	7·4	0·6	1·3	+40·5
Totals 1933	190	0–4340		0·0–70·0		592·6	905·5	46·7	74·2	
Totals 1931–33	538	0–4340		0·0–70·0		2093·5	2254·6	159·8	169·8	

* Wherever possible, the periods selected have been limited to half-months of 15 or 16 days. Occasionally, in order to include as much of the data as we could, we have included a few days which would have otherwise been omitted at the beginning or the end of a period.

CALANUS-HERRING CORRELATIONS.

We will first describe briefly the distribution of Calanus and the nature of its relationship with the herring, and then discuss the significance of the correlations. The seasonal distribution of the samples is shown in Tables I and III whilst Figs. 6, 8, 10, 12 and 14 show their distribution in space during each period of the season in the Shields fishery.

Shields : 1931.

We were unable to begin work in this area before the 29th June so that we have no samples for the early part of the fishery which began at the end of April. Between the 7th and the 28th June however, thirty trials were made with the standard Indicator alongside drifters fishing in this area, by Mr. Michael Graham and Dr. W. G. Hodgson of the Ministry of Agriculture and Fisheries, on a cruise of the R.S. *Onaway*.* We are indebted to them for kindly placing at our disposal their records of Calanus numbers together with the corresponding catches of herring.

The average numbers of Calanus for June, July and August were 90, 70 and 80 respectively (see also Column 4, Table I). In May of the same year Gardiner (1933), using the Indicator in the area for studying the vertical distribution of Calanus, found it at similar depths a little more numerous on the whole than we did later.† From June on to the early part of September a weekly average of under 100 Calanus was the rule.

From the 7th June onwards, we have material (134 samples) for correlating the numbers of Calanus caught by the Indicator with the associated catches of herring. The method and the reasons for its adoption have been explained in Part I (p. 161). The series of samples was divided into half-monthly periods as nearly as possible.‡ The samples for each period were then arranged in ascending order of Calanus numbers and divided into two equal sets : one half containing the lower Calanus numbers of the series and the other the higher numbers (these will in future be termed "poorer" and "richer" Calanus samples). Against each was placed the corresponding catch of herring in crans§ : thus we can estimate the total or average catch of herrings in the poorer Calanus water and compare it with that in the richer. Reference should be made to the examples on pp. 162–3 in Part I. Table I summarises the essential data obtained in this way for all such period tables in the Shields fishing during the three years, and Figs. 5, 7, 9, 11, 13 and 15 (in the next section, pp. 190 to 201) illustrate these tables in a graphical form.

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* See page 51, Report on Sea Fisheries for 1931 (1932).

† See also p. 219.

‡ See footnote to Table I.

§ A cran is a commercial measure of herring by volume. It is equivalent on an average to approximately 1,000 fish, but at different times and in different fisheries it may vary from somewhat less to considerably more.

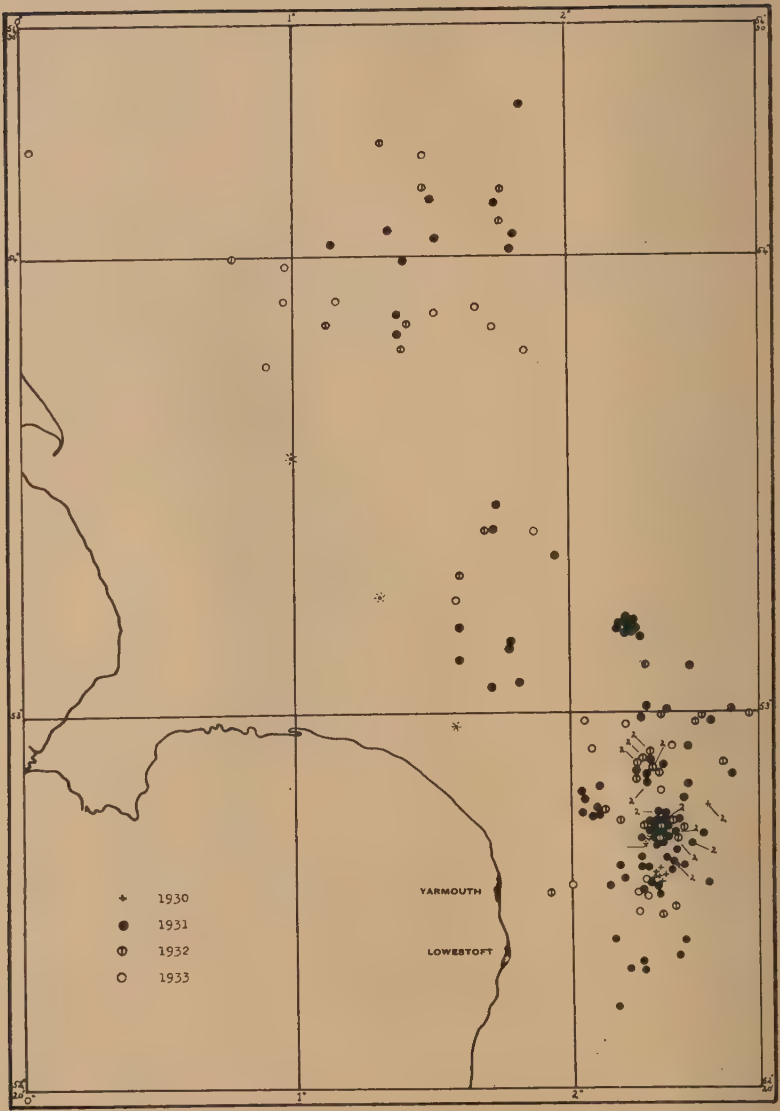
1°
2°
54°
53°
YARMOUTH
LOWESTOFT
+ 1930
● 1931
⊕ 1932
○ 1933

FIG. 4.—Showing the distribution of the Indicator samples in the Humber and East Anglian fisheries during the years 1930–33. Two catches associated with one plankton sample shown thus——2. Light vessels indicated thus *.

The tables in full, together with records of those remaining samples that could not usefully be grouped into tables (see p. 187) and the details of the catches in the Humber area and the Southern Bight, are to be filed in the British Museum (Natural History) and the Library of University College, Hull, and will be available for future workers if required. The series of maps (Figs. 6, 8, 10, 12 and 14) shows the spatial distribution of the Calanus samples over the three years, with the upper and lower halves of the series contrasted by different signs in each period. Alongside these maps are shown also charts of the distribution of the herring catches, the upper, intermediate and lower catches being distinguished by different symbols in each period.

Table I and Fig. 5 show that in June, 1931, when the R.S. *Onaway* samples were taken, a positive correlation was suggested. Thirty samples showed a total of 165·75 crans of herring taken in the poorer Calanus waters and 218·0 crans in the richer Calanus waters, giving an average of 11·1 and 14·5 crans respectively. In the following three half-months the data suggested an increasingly negative correlation (July and the first half of August). Details of the tables (see Figs. 5 and 7) show that the heavier catches were to be found near the lower end of the Calanus series; particularly is this so in the second half of July. The period 16th August–8th September suggested a small positive correlation. So far the general indications appear to be negative, 1087·9 crans being caught in the poorer Calanus waters and 819·0 crans in the richer Calanus waters, but it will be seen later that the use of such totals is subject to objection.

Shields : 1932.

A series of 218 samples was obtained, extending throughout the fishery from the beginning in early May, until the end of August, except for a period (July 21st to August 6th) during which all those drifters using the Indicator went north to the Scottish fishery. Calanus is by far the most important copepod throughout most of the season; its maximum period of abundance was in June (averaging about 1000 per disc) and where comparison is possible (see Table I and Fig. 21) it is much more abundant than in 1931 except at the end of August. The same, however, does not hold for the herring which were mainly scarce in 1932 (Table IV and Fig. 16).

The nature of the correlations between Calanus and the herring is seen in Table I and Figs. 9 and 11. From early May to mid-July they were markedly positive, although much less so in June than in May or July. The second week of August (providing only 11 samples) shows a marked negative correlation, but the latter half of August is again positive. The season as a whole shows a positive correlation, a total of 413·0 crans being caught in the poorer Calanus waters and 530·0 crans in the richer: in this respect 1931 and 1932 differ, but they show similarity in that the largest negative correlations occur in the first half of August in both years.

Shields: 1933.

We obtained this year a complete series of observations from the end of April to the end of August, although the number of samples (193) was somewhat lower than in 1932. Calanus was again the most important copepod, but its distribution in time was a little different from that in 1932. In early May it was quite dense in our samples and averaged about 650 per disc: the number of samples was, however, rather small. Its numbers then decreased steadily until early June when an average of only 41 was found. By the end of the first week in July the numbers had increased to over 1000 and such numbers were maintained till the end of the third week; a sudden drop then produced an average of less than 100 throughout August. It seems probable that on the whole Calanus was richer this year than in 1932 and the landings of herring appear to have been a little heavier (Figs. 16 and 21). The correlations proved to be positive with the exception of the period 16th–30th June (in particular the third week of June) which was decidedly negative (Table I and Figs. 13 and 15). Taking the season as a whole there is a marked positive correlation: 592·6 crans being caught in the poorer Calanus waters and 905·5 crans in the richer waters which were sampled. The most striking difference from the previous years is that the negative correlation so marked in the first half of August of 1931 and 1932, is not apparent this year.

Shields: 1931–33.

The Shields area has been sampled more intensively and for a longer period than those off the Humber and East Anglia, and for that reason we must discuss it in more detail. The totals at the feet of columns 7 and 8 in Table I show that over the three years 2093·5 crans were caught in the poorer Calanus waters (as shown period by period) and 2254·6 crans in the richer waters. As a whole this suggests a general positive correlation between Calanus and the herring, but the figures so obtained are subject to the criticism that they are seriously weighted by the number of samples we were able to obtain in any one period. Thus an average of 18 crans in the first half of July, 1931, is only represented (and so weighted) by 21 samples whereas the average of 2 crans in the first half of June, 1933, is represented by 40 samples and thus is given nearly twice the weight of the previous example. Consequently, in order to evaluate the relationship over the three years and to include all the fluctuations in the abundance of the fish, we thought it advisable to give the results the same weight for each period, as though an equal number of samples was obtained in each. Columns 9 and 10 show the *average* number of crans obtained in lower and higher Calanus waters. They can be taken to be a measure of the results which would be obtained if a constant number of boats had fished a constant number of times in each half-month. Totals obtained from these columns show that in 1931 the correlation was negative with 80·3 crans in the poorer Calanus waters against 59·8 crans in the richer waters. 1932 and 1933 are both positive with figures of 32·8 and 46·7 crans in the poorer waters and 35·8 and 74·2 crans in the richer. The whole shows 159·8 crans in the poorer waters and 169·8 crans in the richer. Now our sampling in the year 1931 was incomplete; the only samples we have for the first half of the season are those taken by the R.S. *Onaway* during June. The sum of the two complete seasons 1932 and 1933, comprising 411 samples taken throughout the two seasons, gives 79·5 crans and 110·0 crans in the poorer and richer Calanus waters respectively.

There are 20 half-monthly periods* in the Shields area and of these 15 show a positive correlation: in itself this might be taken as indicating a 3 to 1 chance that any correlation would prove positive.† A similar ratio of 3 to 1 in the Scottish waters would tend to confirm this possibility, but there is some evidence to show that in the Shields area the negative correlations are limited to a short period. Up to the end of June over the three years, only one result in nine is negative. The first half of July shows one negative and two positive; the second half of July shows one negative and one positive; August 1st–15th shows two negative and one positive whilst all the results from the second half of August are positive. The positive correlation tends to give place to a negative one and then to a positive one again.

The Shields material can be considered in another way. So far we have been using together all the samples collected by different boats in any one period. Now we have seldom had more than five boats using the indicator at one time in this area, and most of the boats have worked over several periods in one or more years. Thus it is possible (as it is not in the other areas) to obtain correlations based upon "Individual Boat" returns, a list of which is shown in Table II. The data have been treated in the same manner as the preceding, but sometimes more irregular periods had to be employed, some extending to as much as one month, or overlapping from one month to the next. This was necessary because the number of samples per individual boat per half-month is sometimes very low. We have omitted from the table any correlation containing less than ten samples, having decided, as in the Scottish area, that ten is the lowest number upon which a correlation may be satisfactorily based.

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* See footnote to Table I.

† It must be borne in mind that only three results are possible for a correlation of this type: positive, negative and identity.

TABLE II.

Summary of Data relating to the Calanus-Herring Correlations based on the Results of the Individual Drifters (A–G) using the Indicator in the Shields Fishery in 1931, 1932 and 1933.

Drifter.	Month and Year.	No. of samples.	Calanus-herring Correlations. Total crans of herrings corresponding to lower and higher Calanus values.		Average crans of herrings corresponding to lower and higher Calanus.		Per cent gain or loss.
			Lower.	Higher.	Lower.	Higher.	
A.	1–15 July, 1931	11	94·8	116·8	17·2	21·2	+10·0
	16–31 July, 1931	17	190·1	90·1	22·4	10·6	−35·7
	1 Aug.–8 Sept., 1931	22	54·5	102·0	5·0	9·3	+30·4
	1–31 May, 1932	18	10·4	22·1	1·2	2·5	+36·2
	1–15 June, 1932	13	17·9	26·1	2·8	4·0	+18·8
	16 June–8 July, 1932	15	34·0	65·5	4·5	8·7	+31·7
	1–31 Aug., 1932	17	26·8	48·0	3·2	5·7	+28·4
	29 April–15 May, 1933	14	35·5	46·5	5·1	6·6	+13·4
	16 May–20 June, 1933	18	37·5	50·0	4·2	5·6	+14·3
	1–31 Aug., 1933	11	14·3	59·3	2·6	10·8	+61·2
	Total Boat A	156	515·8	626·4	68·2	85·0	..
	Average Boat A	16	51·6	62·6	6·8	8·5	+20·9
B.	16–31 July, 1931	10	123·0	111·0	24·6	22·2	− 5·1
	1 Aug.–1 Sept., 1931	20	120·0	117·0	12·0	11·7	− 1·3
	16–31 May, 1932	11	3·8	23·4	0·7	4·3	+71·8
	1–15 June, 1932	11	20·3	38·8	3·7	7·1	+31·4
	16 June–16 July, 1932	12	5·0	25·5	0·8	4·3	+67·2
	Total Boat B	64	272·1	315·7	41·8	49·6	..
	Average Boat B	13	54·4	63·1	8·4	9·9	+32·8
C.	29 July–1 Aug., 1931	17	166·4	121·9	19·6	14·3	−15·4
	1–31 May, 1932	11	12·0	31·5	2·2	5·7	+44·8
	1–30 June, 1932	14	39·0	24·3	5·6	3·5	−23·3
	1–31 July, 1932	10	14·5	29·0	2·9	5·8	+33·3
	Total Boat C	52	231·9	206·7	30·3	29·3	..
	Average Boat C	13	58·0	51·7	7·6	7·3	+ 9·9
D.	12–31 May, 1932	16	19·8	50·8	2·5	6·3	+44·0
	1–15 June, 1932	10	14·8	21·3	3·0	4·3	+18·1
	16 June–13 July, 1932	19	37·8	23·0	4·0	2·4	−21·8
	1–30 June, 1933	21	55·0	72·5	5·2	6·9	+13·7
	1–15 July, 1933	11	69·0	52·0	12·6	9·5	−14·0
	16 July–1 Aug., 1933	15	38·0	102·0	5·1	13·6	+45·7
	Total Boat D	92	234·4	321·6	32·4	43·0	..
	Average Boat D	15	39·1	53·6	5·4	7·2	+14·3
E.	18 May–15 June, 1932	12	20·0	28·5	3·3	4·8	+17·5
	16 June–10 July, 1932	14	40·0	49·0	5·7	7·0	+10·1
	Total Boat E	26	60·0	77·5	9·0	11·8	..
	Average Boat E	13	30·0	38·8	4·5	5·9	+13·8
F.	1–30 June, 1933	22	83·5	39·5	7·6	3·6	−35·8
	1–31 July, 1933	15	134·0	201·0	17·9	36·8	+20·0
	1–15 Aug., 1933	10	20·0	70·0	4·0	14·0	+55·6
	Total Boat F	47	237·5	310·5	29·5	44·4	..
	Average Boat F	16	79·2	103·5	9·8	14·8	+13·3
G.	1–30 June, 1933	20	40·5	82·0	4·1	8·2	+33·9
	Grand total	457	1592·2	1940·4	215·3	271·3	..

The drifters will not be referred to by name but by the letters "A" to "G," since boat owners and skippers may not wish the details of their fishing to be made public. Of the seven boats working for us at different times, six showed a positive relation between Calanus and the herring over the whole time of sampling: one boat C, showed a small negative result.* If the average catches† for the seven boats are added on either side (i.e., totals corresponding to the lower and higher Calanus numbers), as might be expected, a marked positive result is found. Altogether the samples of the seven boats have been arranged into 31 boat-periods: of these 23 proved positive and 8 negative. Here again is the ratio of three positive results to one negative one, but again the negative results are seasonal: May shows positive results only, in June nine out of eleven are positive, in July less than half are positive whereas in August four out of five are positive. The negative period is July, and mainly in the second half of the month, but it will be remembered that the previous results suggest August 1st–15th as the most negative period. It is possible that the difference between these results is due to the insufficiency of samples in August to provide half-monthly individual boat results, and the probable overweighting of the negative tendencies in early August by the definitely positive ones in late August when these periods are combined. In weighing up these results we must not forget that no negative correlations were found in the late July and August periods of 1933.

The Shields material may also be considered with regard to the spatial relationships between Calanus and the herring. We have already referred to the series of charts (Figs. 6, 8, 10, 12 and 14) showing the distribution of the Shields samples during each half-month for the three seasons. They have been arranged in pairs, one of each pair showing the broad distribution of Calanus and the other that of the associated catches of herring. In the Calanus charts the open circles indicate the lower and the filled-in circles the upper halves of the Calanus series respectively (based on the correlation tables described on p. 161 of Part I and p. 183 of this part). In the herring charts a little more detail is shown: the catches have been arranged in an ascending series as with Calanus, and then divided into three sections such that the open circles show the lower half of the catches, whilst the upper half (shown as shaded and filled-in circles) has again been divided, into two sections, the shaded circles representing the third quarter and the filled-in circles the top (fourth) quarter of the ascending series of catches.‡ This series of charts represents the first continuous survey of conditions on a herring ground over three seasons and permits a broad comparison to be made of the spatial distribution of Calanus and the herring period by period. To further this comparison, histograms representing the period correlation tables (see p. 183) have been arranged facing each appropriate pair of charts (Figs. 7, 9, 11, 13 and 15). The sets of spatial diagrams and histograms should be

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* This is found to be positive when treated another way. (See p. 215.)

† See note on p. 187.

‡ Odd numbers and the coincidence of several identical values of Calanus or herring at the half or three-quarter points in the ascending series may (as in the period 1–15 May, 1932) necessitate the halves or quarters of the series being only approximate.

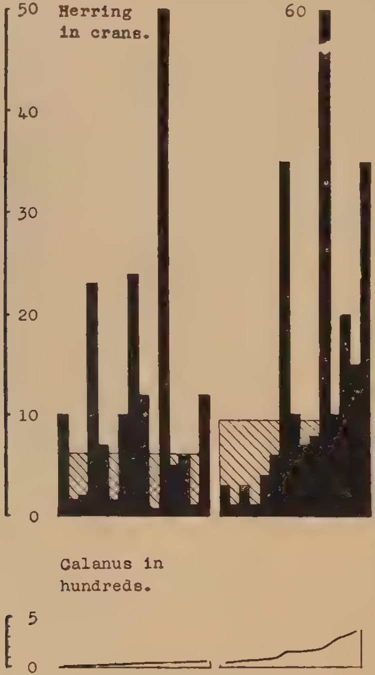

FIG. 5.—Histogram showing (in black) the individual catches of herring in June, 1931, arranged from left to right in the order of the ascending values of Calanus in the associated plankton Indicator samples. The series is divided into halves, the left half representing the catches in the poorer Calanus water and the right half the catches in the richer Calanus water. The average catches of herring in each half are shown as shaded histograms. Below are graphs showing the associated Calanus values.

considered together. At first sight the correspondence between the distribution of the herring and that of Calanus may not appear to be a close one, but a study of the histograms will show that usually the highest catches of herring are taken in the highest Calanus areas. In the small spatial charts it has been impossible to indicate the relative sizes of the catches in the higher Calanus water.

In general the series of charts and histograms needs little description in the text, but certain features seem worthy of mention. As a whole there is a fair correspondence in the spatial distribution of the higher Calanus samples and the higher catches except in certain periods when the charts show how inadequate has been the sampling of the area (e.g. the period 1–15 August, 1932) and when (particularly with a generally high or low average value of Calanus) the higher Calanus values are distributed widely over the whole area (this is particularly well shown in the two June periods of 1932 during which the positive correlations were almost negligible).

In 1931 the samples showed Calanus to be very sparse and evenly scattered in the area during July and the first half of August : in early July there appeared to be a concentration of herring in the centre of the area, but in late July and early August the herring also were fairly evenly spread and relatively large numbers were on the grounds. At the end of the season (16 August–8 September) there was a definite concentration of Calanus near the coast and some concentration of the herring in that region also : the correlation for this period was only slightly positive. The spatial distribution of Calanus as a whole during July and August does not suggest that it would be possible for the herring to locate dense patches even if the feeding urge was great, and we do indeed find by correlation a generally negative association during these periods (but see also p. 223).

In early May, 1932, we had relatively few scattered samples, but individually the association between the samples and their catches was very good. Later in May there is definitely a concentration of herring in the richer Calanus area. The June periods have been mentioned above. In July we obtained no samples after the 20th, but up to that date there is a good correspondence, six out of eight of the highest catches being found in the higher Calanus zones (mainly on the eastern side of the fishing area). The late August samples (for reference to early August, see above) suggest that both Calanus and the herring were more abundant in the northern part of the fishery.

In 1933 the correspondence is closer. In May there were relatively few scattered samples, with both Calanus and the herring irregularly distributed. In early June, whilst both are still diffuse, there is a rather closer agreement in distribution. The period 16–30 June shows an interesting feature. We see in the corresponding histogram in Fig. 13 that the correlation for this period was negative, but that when split into two sub-periods the first (16–22 June) is negative and the second (23–30 June) is positive, there being many more Calanus in the second sub-period than in the first. Referring to the charts, the southern group of samples and the most northerly ones in general represent the first sub-period whilst the second sub-period has samples mainly in the centre of the area. It seems possible

[*text continued on p. 202.*]

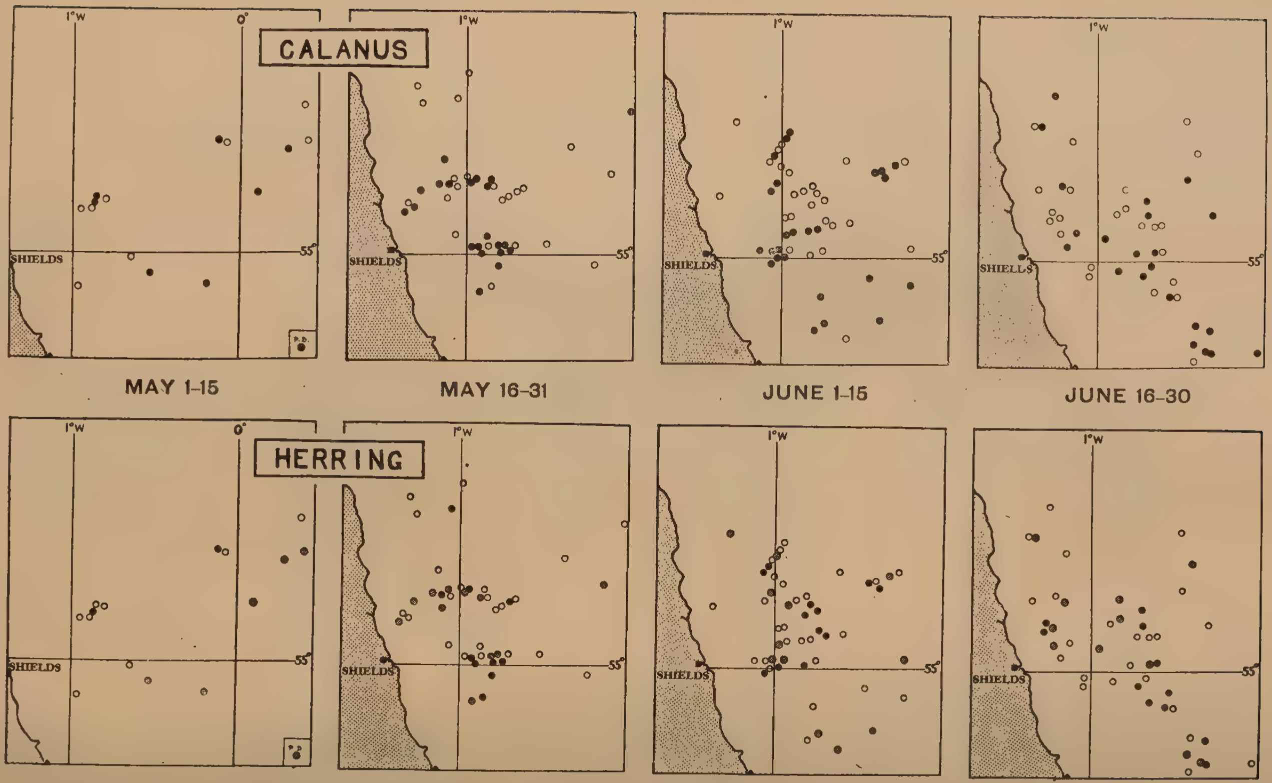

FIG. 8.—Charts showing the half-monthly distribution of Calanus as sampled by the Indicator in May and June, 1932, and below them the associated catches of herring. In the Calanus charts those samples falling in the upper half of an ascending series of Calanus values are shown as blacked-in circles and those in the lower half as open circles. In the herring charts the catches have been arranged in an ascending series as with Calanus but divided into three sections: the lower half of the catches shown as open circles, and the upper half again divided into two quarters shown as shaded and blacked-in circles, the latter representing the highest values. P.D. indicates position doubtful.

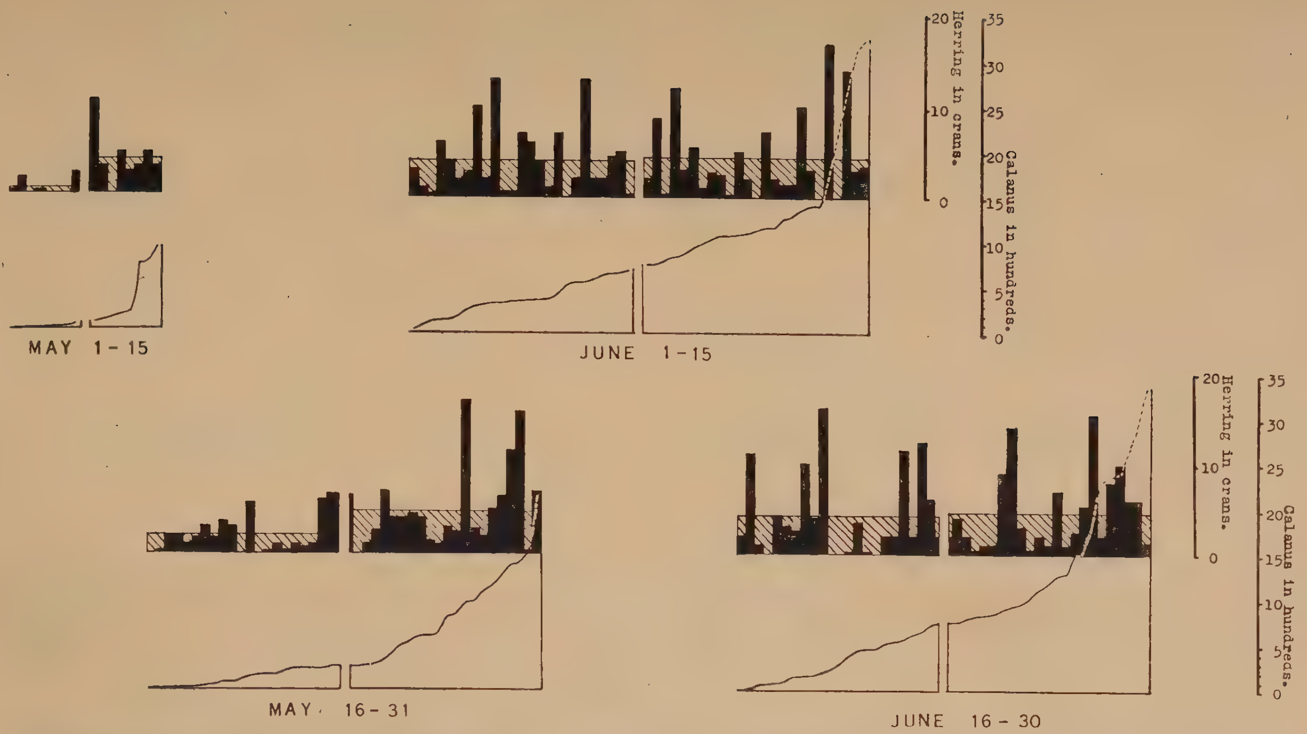

FIG. 9.—Histograms showing (in black) the individual catches of herring in the half-monthly periods corresponding to the charts in Fig. 8, arranged in each period from left to right in the order of the ascending values of Calanus in the associated plankton Indicator samples. Each series is divided into halves, the left half representing the catches in the poorer and the right half the catches in the richer Calanus water. The average catches of herring in each half are shown as shaded histograms. Below each histogram is a graph showing the associated Calanus values. The diagrams are in fact graphical representations of the period tables drawn up for correlation purposes. For discussion, see text.

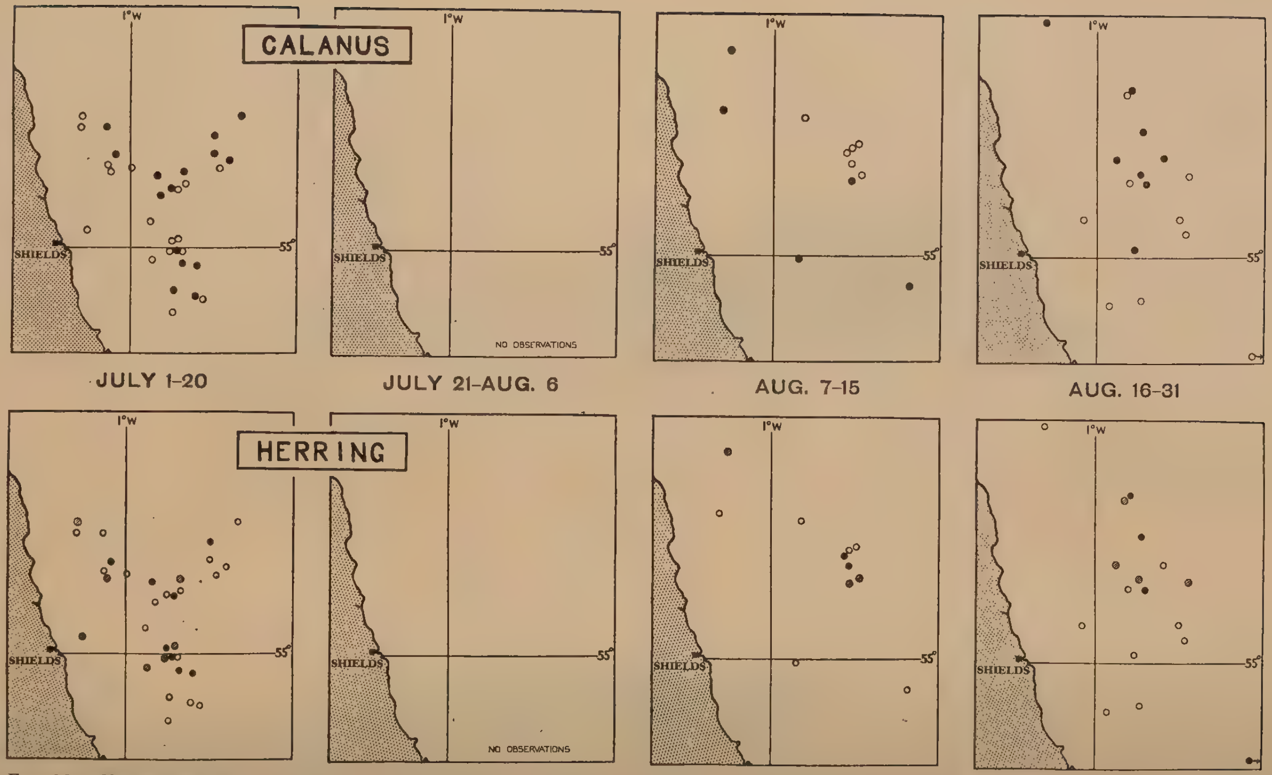
CALANUS
HERRING
1°W
55°
SHIELDS
NO OBSERVATIONS
JULY 1–20
JULY 21–AUG. 6
AUG. 7–15
AUG. 16–31

Fig. 10.—Charts showing the half-monthly distribution of Calanus as sampled by the Indicator in July and August, 1932, and below them the associated catches of herring. In the Calanus charts those samples falling in the upper half of an ascending series of Calanus values are shown as blacked-in circles and those in the lower half as open circles. In the herring charts the catches have been arranged in an ascending series as with Calanus, but divided into three sections: the lower half of the catches shown as open circles, and the upper half again divided into two quarters shown as shaded and blacked-in circles, the latter representing the highest values.

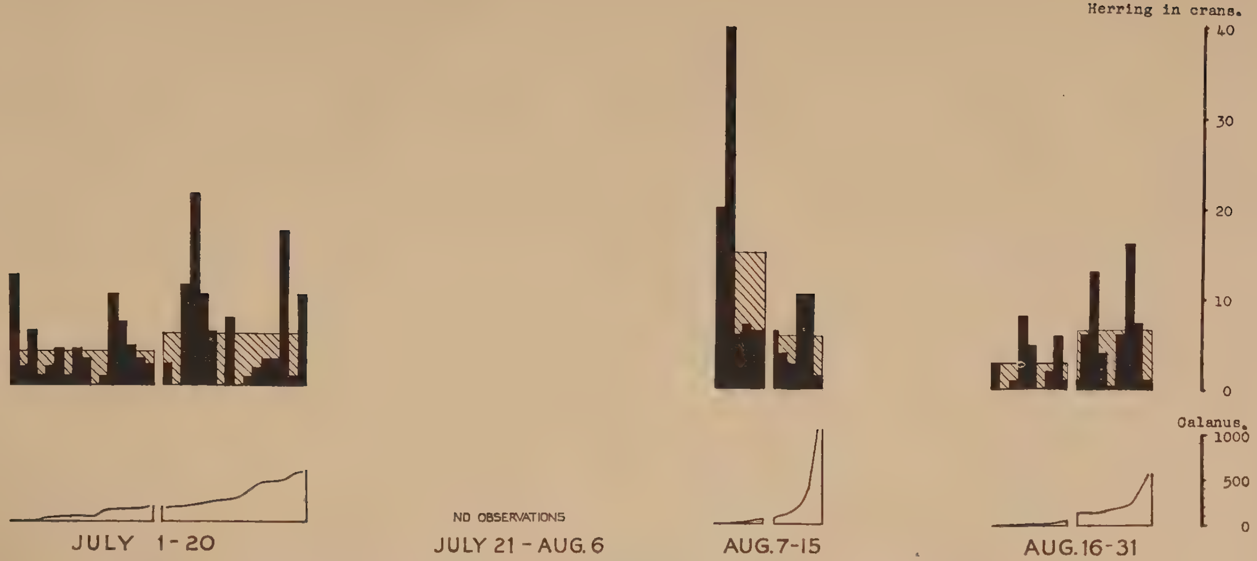

FIG. 11.—Histograms showing (in black) the individual catches of herring in the half-monthly periods corresponding to the charts in Fig. 10, arranged in each period from left to right in the order of the ascending values of Calanus in the associated plankton Indicator samples. Each series is divided into halves, the left half representing the catches in the poorer and the right half the catches in the richer Calanus water. The average catches of herring in each half are shown as shaded histograms. Below each histogram is a graph showing the associated Calanus values. The diagrams are in fact graphical representations of the period tables drawn up for correlation purposes. For discussion, see text.

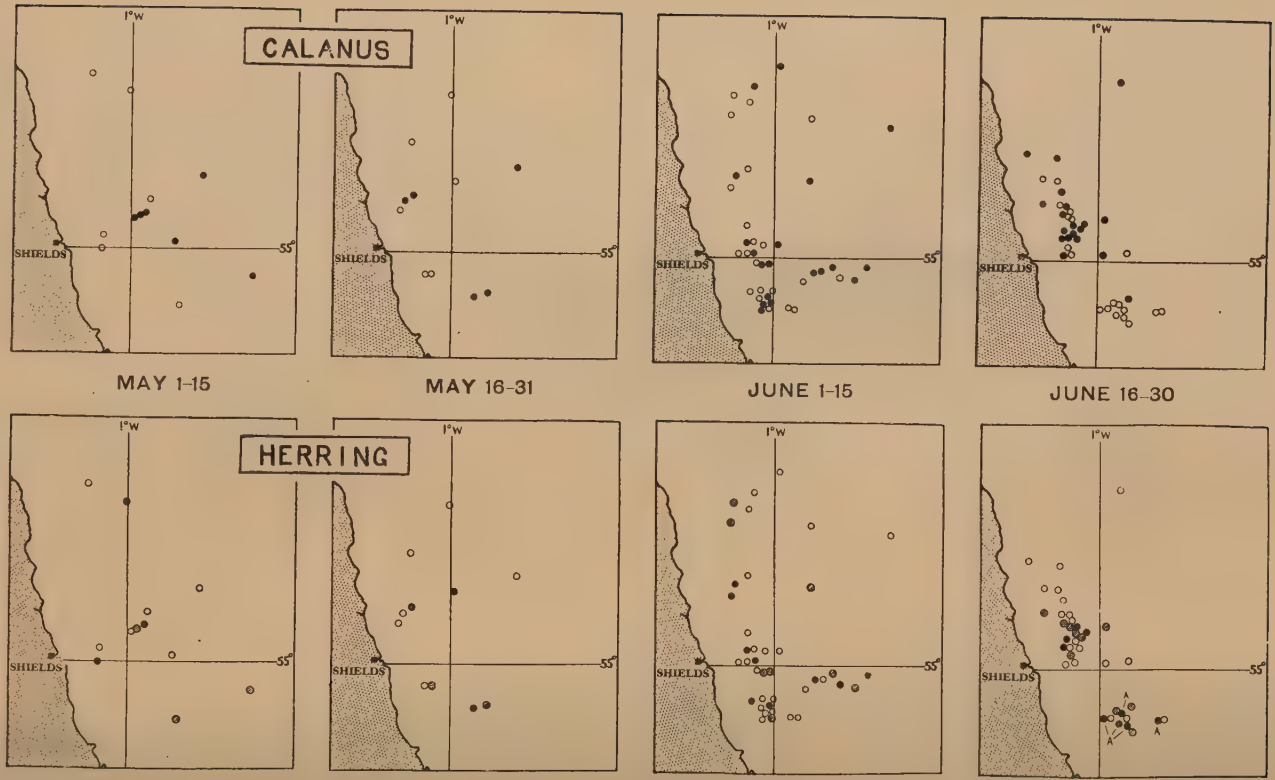

FIG. 12.—Charts showing the half-monthly distribution of Calanus as sampled by the Indicator in May and June, 1933, and below them the associated catches of herring. In the Calanus charts those samples falling in the upper half of an ascending series of Calanus values are shown as blacked-in circles and those in the lower half as open circles. In the herring charts the catches have been arranged in an ascending series as with Calanus, but divided into three sections: the lower half of the catches shown as open circles, and the upper half again divided into two quarters shown as shaded and blacked-in circles, the latter representing the highest values.

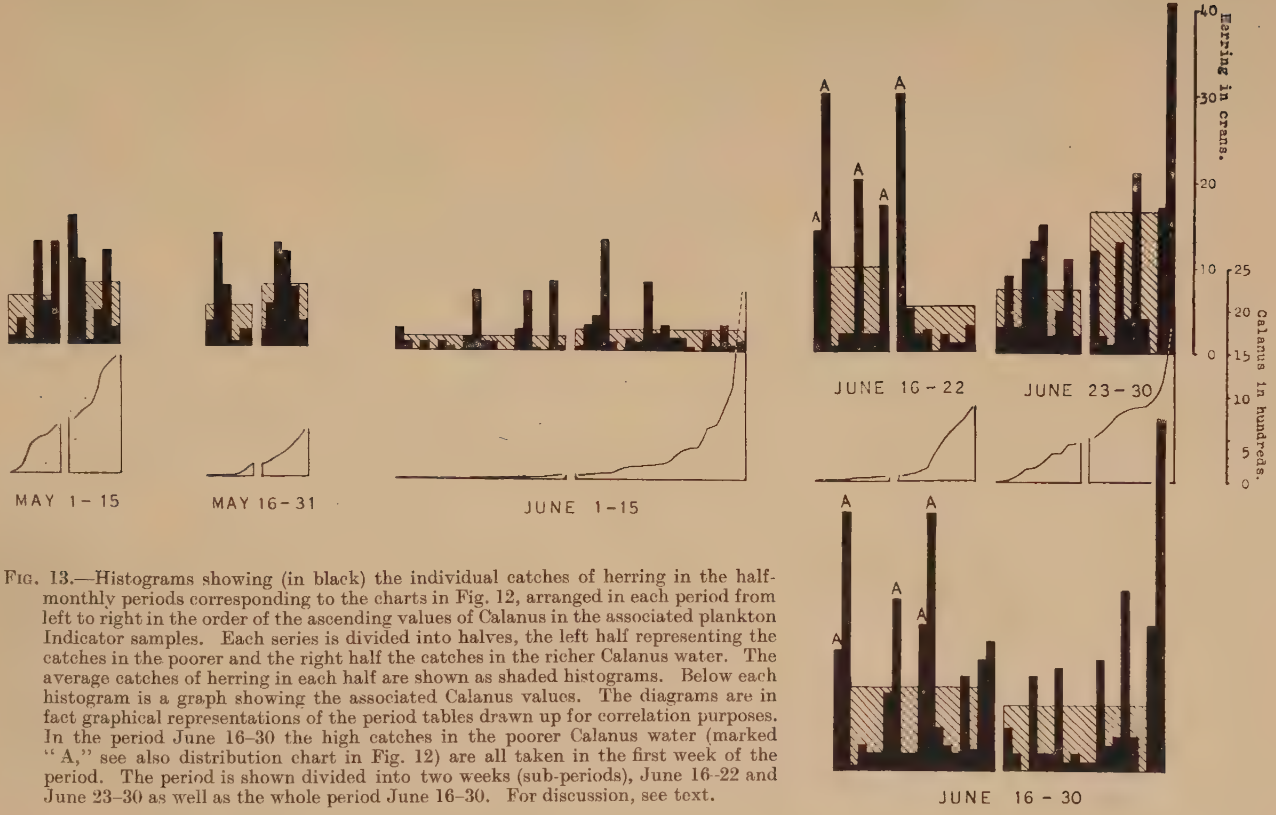

FIG. 13.—Histograms showing (in black) the individual catches of herring in the half-monthly periods corresponding to the charts in Fig. 12, arranged in each period from left to right in the order of the ascending values of Calanus in the associated plankton Indicator samples. Each series is divided into halves, the left half representing the catches in the poorer and the right half the catches in the richer Calanus water. The average catches of herring in each half are shown as shaded histograms. Below each histogram is a graph showing the associated Calanus values. The diagrams are in fact graphical representations of the period tables drawn up for correlation purposes. In the period June 16–30 the high catches in the poorer Calanus water (marked "A," see also distribution chart in Fig. 12) are all taken in the first week of the period. The period is shown divided into two weeks (sub-periods), June 16–22 and June 23–30 as well as the whole period June 16–30. For discussion, see text.

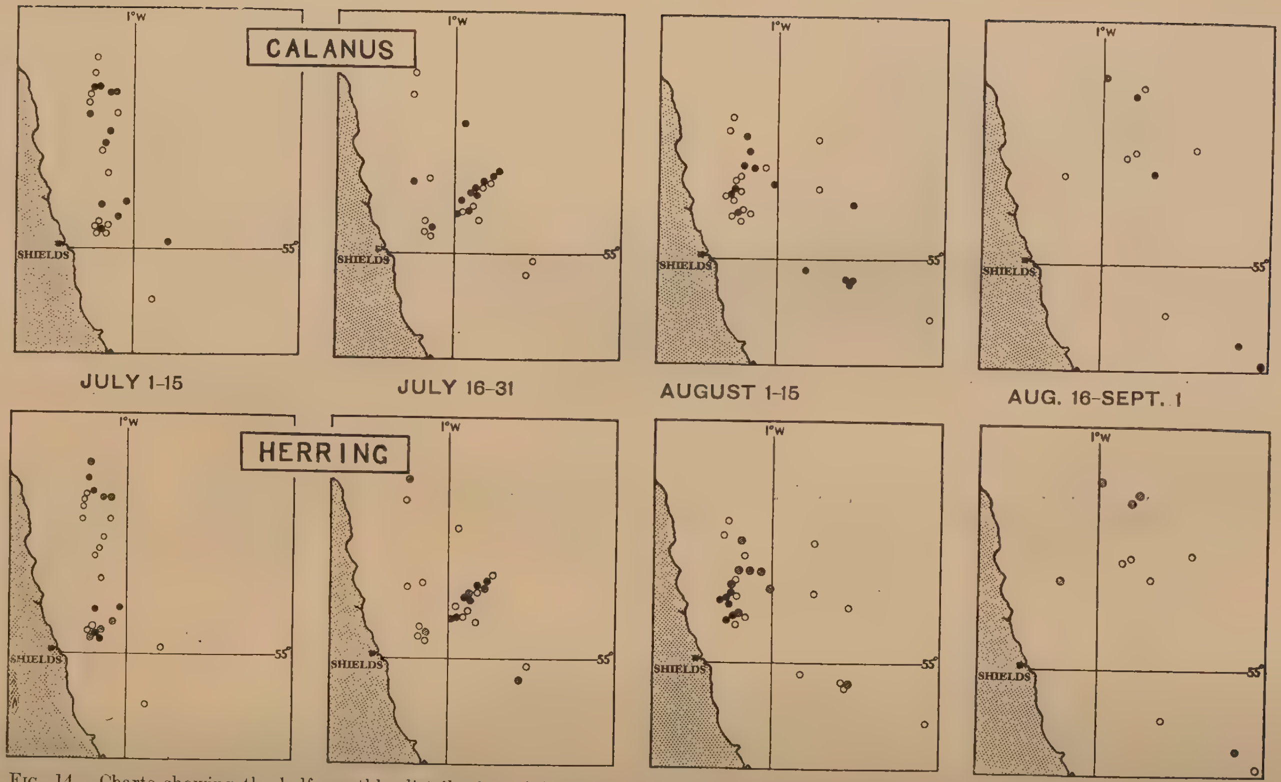

FIG. 14.—Charts showing the half-monthly distribution of Calanus as sampled by the Indicator in July and August, 1933, and below them the associated catches of herring. In the Calanus charts those samples falling in the upper half of an ascending series of Calanus values are shown as blacked-in circles and those in the lower half as open circles. In the herring charts the catches have been arranged in an ascending series as with Calanus, but divided into three sections: the lower half of the catches shown as open circles, and the upper half again divided into two quarters shown as shaded and blacked-in circles the latter representing the highest values.

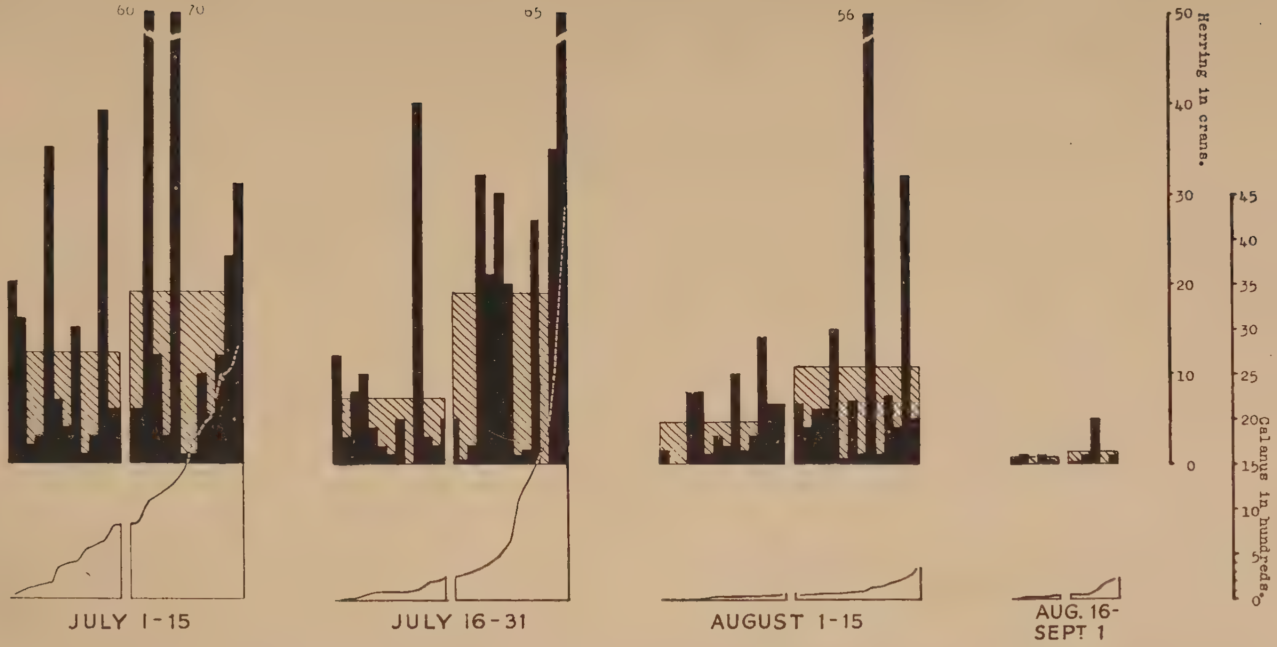

FIG. 15.—Histograms showing (in black) the individual catches of herring in the half-monthly periods corresponding to the charts in Fig. 14, arranged in each period from left to right in the order of the ascending values of Calanus in the associated plankton Indicator samples. Each series is divided into halves, the left half representing the catches in the poorer and the right half the catches in the richer Calanus water. The average catches of herring in each half are shown as shaded histograms. Below each histogram is a graph showing the associated Calanus values. The diagrams are in fact graphical representations of the period tables drawn up for correlation purposes. For discussion, see text.

that a shoal entering the area in the third week of June did not find the richer Calanus zone (more central) during that week and a negative correlation resulted, whilst in the fourth week the higher catches were definitely to be found in the richer Calanus waters, a positive correlation resulting. In early July again there is a general correspondence and in the later part of the month we find the best example of coincidence, the herring being mainly limited to a small area of relatively dense Calanus. In early August there is some correspondence, with the herring limited more to the western side of the fishery : later in the month the samples are too few and scattered to reveal any relationship, although the correlation diagram suggests a marked positive association.

From consideration of all the foregoing results, we are able to conclude that over the three years 1931–33, there is on the whole a positive correlation between Calanus and the herring the commercial significance of which will be discussed presently. There are certain negative results, and in 1931 and 1932 these are mainly confined to July and August : these may be accidental variations in the general relationship perhaps arising out of inadequate methods of investigation, but they probably have a more significant meaning. This matter will also be discussed later.

Humber Area : 1931–33.

Towards the end of the Shields season there is a tendency for the drifters to move in towards the coast and some move southwards towards the Humber mouth. The area fished at this time is quite distinct from that of the earlier Shields fishery which we have been considering and which is often being fished at the same time : we have delimited this area by the lines of latitude 53° 00′ N. and 54° 20′ N. During August and September we have received samples taken in this area by drifters sailing from both Shields and Yarmouth. Table III shows details of the correlations from this ground.

In September, 1931, Calanus was even scarcer than it was further north, but 16 samples show a positive correlation. There are only 19 samples spread over October, November and December, and no useful correlations can be made for even a whole month.

In 1932 Calanus appeared to be scarce, but since only eight samples were returned in September the positive correlation, whilst suggesting a confirmation of the previous year's result, must not be given much weight. There are only four records from October to December.

Calanus was scarce in 1933 and the material not suitable for correlation purposes : there are only nine samples for September and the results are heavily weighted by a single large catch of 142 crans.

TABLE III.

SUMMARY OF THE DATA RELATING TO THE CALANUS-HERRING CORRELATIONS BASED ON THE RESULTS FROM ALL DRIFTERS USING THE INDICATOR IN THE HUMBER AND EAST ANGLIAN FISHERIES IN 1930, 1931, 1932 AND 1933.

Period and Year.	Number of samples.	Calanus range.	Average Calanus.	Herring range.	Average herring.	Total number of herring in crans corresponding to lower and higher Calanus values.		Average number of herring in crans corresponding to lower and higher Calanus values.	
						Lower.	Higher.	Lower.	Higher.
				Humber Area.					
September, 1931	16	0–32	12	0·0–95·0	20·9	127·4	206·8	15·9	25·8
October, 1931	7	0–84	36	1·0–102·0	28·3	33·0	165·0	9·4	47·1
November, 1931	6	0–1	0	2·5–53·0	24·4	†	†	†	†
December, 1931	6	0	0	8·0–43·0	15·7	†	†	†	†
September, 1932	8	0–530	81	1·0–20·0	4·1	10·4	22·5	2·6	5·6
October, 1932	1	10	10	50·0	50·0	†	†	†	†
November 1932,	1	0	0	36·0	36·0	†	†	†	†
December, 1932	2	10	10	3·0–50·0	26·5	†	†	†	†
September, 1933	9	4–105	31	0·3–142·0	16·6	143·5	5·4	31·9	1·2
October, 1933	2	10–12	11	0·0–1·0	0·5	†	†	†	†
				East Anglian Area.					
October, 1930	7	0	0	12·0–41·0	26·4	*	*	*	*
November, 1930	3	0–1	0	5·0–12·0	8·3	†	†	†	†
October, 1931	26	0–100	17	1·0–82·0	19·1	352·3	143·5	27·1	11·0
November, 1931	40	0–34	3	0·0–76·0	13·3	*	*	*	*
July, 1932	2	0	0	0·0–0·2	0·1	†	†	†	†
October, 1932	7	0	0	4·0–38·0	14·3	*	*	*	*
November, 1932	17	0	0	4·0–42·0	11·2	*	*	*	*
December, 1932	2	0–1	0	11·8–21·5	16·6	†	†	†	†
June–November, 1933	6	0–40	7	0·0–4·0	1·1	†	†	†	†

* There were too few samples with Calanus present in these periods for correlation purposes.

† Correlation tables were not made for periods containing less than seven samples.

East Anglian Area : 1930–33.

The division between this fishery and the Humber fishery is quite arbitrary. As drifters move south fishing may be carried out by a fairly regularly distributed fleet over both areas. As the two together are large, we felt justified in separating a northern (Humber) area characterised by a relatively richer zooplankton and younger earlier spawning herring from a southern (East Anglian) region with a poorer plankton fauna, and a fishery composed of older late spawning fish. The fisheries are also separated in time, the Humber fishery taking place mainly before the East Anglian fishery attains its peak. The position of the samples is shown in Fig. 4 and details of analyses in Table III.

Only one period in this area gives sufficient data to provide a correlation : Table III shows this to be strongly negative. In the remaining periods either the data are too scanty or Calanus is too scarce, but we may note that a positive correlation with Calanus would not be expected in the East Anglian area in October, November and December, since the work of Hardy (1924) and Savage (1931) showed that the herring during this time were not feeding.

TABLE IV.

Showing the Average Catches of Herring in Crans for the Whole Fleet and the Boats using the Indicator, Per Half-Month in the Summer Shields Fishery for 1931, 1932 and 1933.

Date.	1931.		1932.		1933.	
	Fleet.	Indicator boats.	Fleet.	Indicator boats.	Fleet.	Indicator boats.
1–15 May	7·4	–	4·2	2·2^{16}	3·9	6·3^{12}
16–31 May	10·4	–	3·1	3·5^{43}	3·6	6·0^{11}
1–15 June	4·4	2·0^{6}*	3·9	4·1^{50}	3·5	2·1^{40}
16–30 June	14·1	15·5^{24}*	3·7	4·4^{45}	6·7	8·6^{38}
1–15 July†	17·0	18·0^{21}	5·2	4·7^{28}	12·2	15·7^{25}
16–31 July	18·1	19·1^{37}	11·1	6·9^{4}	9·3	13·2^{25}
1–15 August	8·6	11·8^{17}	6·7	10·5^{11}	4·5	7·8^{28}
16–31 August	7·0	9·0^{22}	3·9	4·7^{17}	6·3	1·0^{11}
1–15 September	11·5	5·9^{7}	9·3	6·3^{4}	4·8	–
16–30 September	9·4	–	7·9	–	14·6	–

The index figures against the catches of the Indicator boats denote the number of catches for the period.

The Commercial Significance of the Calanus Correlations.

We may now consider the practical significance to the industry of the Calanus results and in doing so we must confine ourselves to the Shields fishery since we have just seen that in the autumn fishery further south the Calanus are scarce and the herring are not feeding.‡

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* Results supplied from the R.S. *Onaway* (see p. 183).

† This period in 1931 is 29th June–15th July.

‡ In a later part (IV) it will be seen that the Indicator can have considerable commercial value in the Autumn East Anglian fishery on account of the phytoplankton indications.

At first sight it may seem unreasonable to regard the samples collected by at most five boats at one time as representative of the fishery. Mr. Leach, the Ministry of Fisheries District Inspector at Shields, having kindly provided us with the details of the landings at Shields for the three years, we are able to show (Fig. 16) that the average catches of the Indicator boats do follow those of the whole fleet very closely* (see details in Table IV). It is difficult to believe that they are not fairly representative in other matters.

Fig. 16 also enables us to compare the course† and magnitude of the fishery in the three years. The 1931 season (which followed a very poor season in 1930) was much more productive than either of the succeeding years. The total and average catches are as follows :

1931. Total of 57,000 crans, i.e. average of 9·4 crans for 6125 landings.
1932. ,, 25,000 ,, ,, 5·7 ,, 4407 ,,
1933. ,, 33,000 ,, ,, 6·3 ,, 5295 ,,

Accounts in *The Fishing News* show that the larger and better fish appeared somewhat later in each successive year.

In 1931 the Shields herring were small until mid-July, when we read that "the more mature fish are appearing in better proportion" and "many fine fish showing well-developed roes and melts are in the average shot." The quality remained mixed, but seemed to improve as time passed, the season ending on the 6th October. The ports near to Shields on the East coast also showed this improvement over the previous year.

In 1932 *The Fishing News* records that fish were small until mid-July when the quality became somewhat better, but they were still very "mixed" and remained so until mid-August when the best fish of the season so far were obtained. The quality remained good until the end of the fishery (8th October). Catches at the neighbouring ports were much poorer than in 1931.

In 1933, again according to *The Fishing News*, the fish appear to have been very small up to 12th August : then there was an "enormous improvement in quality." Towards the end of the season the fish were again "poor." At the adjacent ports the catches were even poorer than in 1932 : small and poor quality fish were exceptionally evident.

It may be of interest here to quote from the Report on Sea Fisheries for 1933 (1934), page 25 : for the Hartlepool fishery up to September "complaints were general of the scarcity and poor quality of the fish brought in. During the early part of July herrings were small and oily and exceptionally small fish were landed in August. . . ." Again, at Grimsby as "at so many other stations along the East coast, complaints were made of the poor quality of the fish" (p. 26).

In Part I of this account (p. 162) we have shown how the correlations can be evaluated for commercial purposes as percentage gains and losses.

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* The average catches for the whole fleet are based on steam drifters in 1931, but in 1932 and 1933 they also include the landings of the few motor drifters. The drifters using the Indicator were all steam.

† Figs. 6, 8, 10, 12 and 14 show broadly the distribution of the shoals of herring in each half-month period over the three years.

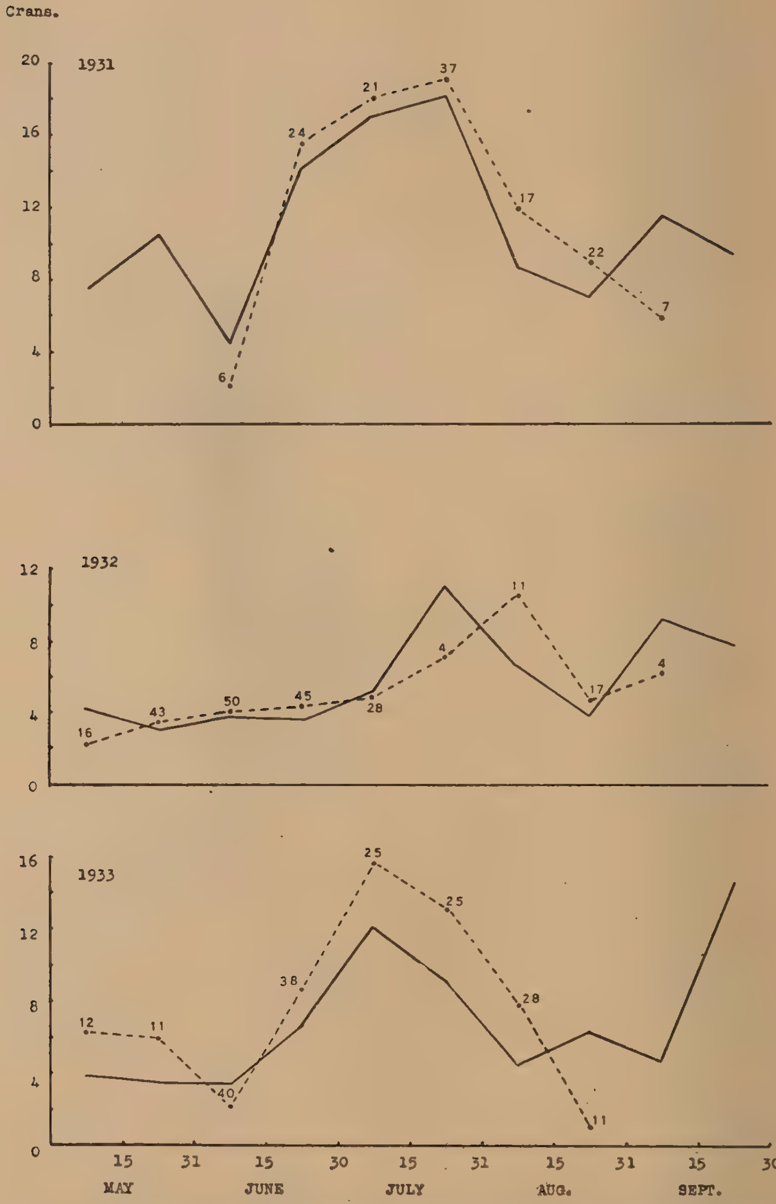

Fig. 16.—Showing for the Shields fishery the average catches per half-month obtained by the drifters using the Indicators (broken line) and those for the whole fleet (continuous line). The index figures denote the number of samples on which the Indicator averages are based.

These percentages have been used to estimate the probable advantages and disadvantages of using the Indicator as a means of locating the herring. As happened throughout the Scottish areas, the Shields samples for 1931 and 1932 were obtained with the Indicator when drifters were fishing without using it to find better fishing grounds. During 1933, however, the skippers had a knowledge of the probable benefits of fishing in waters rich in Calanus and though they were not provided with the proper means of examining the discs, they could recognise Calanus and to some extent use the Indicator for locating better water. It seems reasonable to suppose that had they been using the Indicator as in 1931 and 1932, more shots would have been made in less productive water, and the estimated gains and losses would have been larger. It is noteworthy that as shown in Fig. 16, although in all the three years the average catches of the Indicator boats were as a whole higher than the averages at the port, in 1933 this difference was appreciably larger than in the previous years.

As will be seen, the percentages just referred to can also be used as a general measure of the correlation between Calanus and the herring. This method has the advantage over any other method of presentation in that, being based upon a constant of 100, the fluctuations in the fishery can be eliminated and the results can be applied to the prices of fish in order to give some idea of the monetary value of the instrument.*

In Table I, column 11, are shown the resulting percentage gains and losses based on the catches discussed on page 185 *et seq*. In Fig. 17 they have been expressed in graphical form for the Shields area. These graphs suggest how the efficiency of the Indicator (efficiency in terms of its indication of the presence of herring) may vary throughout the seasons. Extreme caution must be used when considering the individual period results: reference to Figs. 5, 7, 9, 11, 13 and 15 shows that in several periods a single high or low catch may by its position weight unduly the resulting gain or loss. It is the average results for all the twenty periods (a gain of 12·7%) combined with the apparent periodicity of the losses, which is significant. Also the average for each half-month over the three years (shown graphically in Fig. 17 by the broken line) may give some indication of the expected seasonal variations in that it bears some relation to the known variations in the feeding habits of the herring in these waters (see later, p. 218). The results for 1931 represent only a part of the season and when the two complete years 1932 and 1933 are considered alone, the average gain is seen to be 21·2%. It is perhaps even more important to note that by avoiding unsuitable water as revealed by the plankton indications, it should have been possible for a similar quantity

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* Prices tend to vary with the abundance of the fish. As a result it is quite probable that a gain made in using the Indicator during a poor period of fishing, may balance or even exceed any possible loss resulting during a period of heavy fishing when the ruling prices are poor.

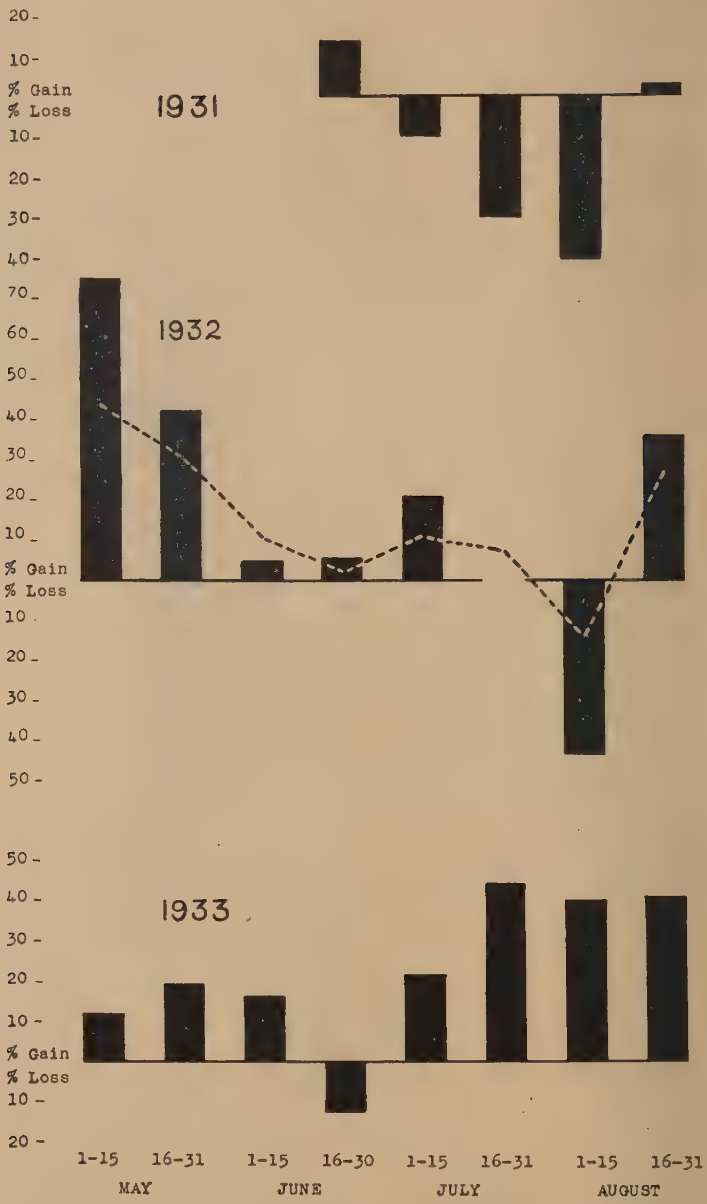

Fig. 17.—Graphical representation of the sequence of the theoretical percentage gains and losses (see text) per half-month period during the three years 1931–33 in the Shields fishery. The dotted line in the central (1932) graph represents the average gain or loss for each half-month over the three years.

of fish to have been caught in the majority of the periods with a total expenditure of less fuel and also fishing time; i.e. with either a smaller fleet or a similar fleet working on fewer days.

Since the percentage gains and losses of less than 10% might be commercially and statistically insignificant, they have been termed "Neutral." Of the twenty half-monthly periods there are twelve which show gains of over 10% (ranging from 11·8% to 75·1%), four neutral periods and four periods showing losses of more than 10% (ranging from 12·6% to 43·6%). These may be set out as follows:

% Gains.	Neutral.	% Losses.
75·1	4·8	− 12·6
43·9	4·4	− 29·9
41·7	3·1	− 40·3
40·5	− 9·7	− 43·6
39·7		
35·3		
21·3		
20·3		
19·1		
16·2		
13·6		
11·8		

This table should be compared with a similar one prepared for the Scottish fishery shown on page 253, where we see that the ratio of percentage gains, neutrals and percentage losses is 11 : 5 : 2 for the "primary" periods.

It has already been stressed that the particular values of the individual periods are of little significance by themselves in that individual catches may be weighting the results. This is shown in Figs. 5, 7, 9, 11, 13 and 15 where the details of the catches for all the periods are shown graphically. We see here that both high and low catches occur in both the richer and the poorer Calanus waters, but on the average there are more higher catches in the richer waters than in the poorer.

Acting on the suggestion of Prof. R. A. Fisher, we have estimated the Standard Error for each of the mean percentage gains shown above. The results may now be expressed as follows:

Year.	No. of periods.	Theoretical mean gain.	Standard error of mean.	Corresponding value for "t."
1931–33	20	12·7%	±6·7%	1·90
1932–33	15	21·2%	±7·5%	2·82

We are greatly indebted to Prof. Fisher for his kind assistance and advice.

We can estimate the frequency with which the larger and smaller catches occur in the richer and poorer Calanus waters respectively. The following table shows this for the three years 1931, 1932 and 1933 separately, for the three years combined and for the two complete years 1932 and 1933 combined, together with the percentages of the catches of 0·0, 0·1–5·0, 5·1–10·0, 10·1–20·0 and over 20·0 crans in the poorer and richer waters respectively.

		Numbers of catches.		Percentage of catches.		
	Herring catch range. Crans.	Poorer Calanus water.	Richer Calanus water.	Poorer water.	Richer water.	Total.
1931	0	1	1	1·5	1·5	1·5
	0·1–5·0	14	**24**	21·6	**37·0**	29·3
	5·1–10·0	**15**	13	**23·1**	20·0	21·6
	10·1–20·0	13	**17**	19·9	**26·1**	23·0
	20·0 and over	**22**	10	**33·9**	15·4	24·6
1932	0	**13**	8	**12·4**	7·6	10·0
	0·1–5·0	**65**	60	**61·9**	57·2	59·6
	5·1–10·0	18	**21**	17·1	**20·0**	18·5
	10·1–20·0	8	**15**	7·6	**14·2**	10·9
	20·0 and over	1	1	1·0	1·0	1·0
1933	0	**10**	6	**10·8**	6·5	8·7
	0·1–5·0	**50**	49	**53·7**	52·6	53·1
	5·1–10·0	**14**	11	**15·1**	11·9	13·5
	10·1–20·0	**14**	13	**15·0**	13·9	14·5
	20·0 and over	5	**14**	5·4	**15·1**	10·2
1932–33	0	**23**	14	**11·6**	7·1	9·4
	0·1–5·0	**115**	109	**58·1**	55·0	56·5
	5·1–10·0	32	32	16·2	16·2	16·2
	10·1–20·0	22	**28**	11·1	**14·1**	12·6
	20·0 and over	6	**15**	3·0	**7·6**	5·3
1931–33	0	**24**	15	**9·1**	5·7	7·4
	0·1–5·0	129	**133**	49·1	**50·6**	49·9
	5·1–10·0	**47**	45	**17·8**	17·1	17·4
	10·1–20·0	35	**45**	13·4	**17·1**	15·3
	20·0 and over	**28**	25	**10·6**	9·5	10·0

Fig. 18 shows graphically for the years 1931, 1932 and 1933 a derivative of this table : i.e. graphs of the percentage of all the catches each year which fall below the given values of 0·1, 5·1, 10·1 and 20·1 crans for the poorer and richer Calanus waters. The essential difference between the year 1931 and the two succeeding years is well shown in this figure where we see clearly that the presence of the higher catches in the richer water and the lower catches in the poorer water generally throughout 1932 and 1933 was reversed on the whole in 1931 (particularly between July 1st and August 15th) ; but we must also note, that for our investigations, the year 1931 was an incomplete season, the bulk of the samples being obtained after the middle of June. Fig. 18 should be compared with Fig. 4 in Part III, page 257, where graphs similarly derived are shown for the Scottish area.

Thus we see that for the combined years 1932–33 there were fewer lower catches and more higher catches in the richer water than in the poorer water. A similar distribution is found for the Scottish fishery (see page 253, Part III). This method of treatment brings out an interesting difference between these fisheries for these two years. In the Shields fishery 1932–33 only 9·4% of the total catches were blank and only 5·3% exceeded 20 crans, whereas in the Scottish fishery, 1932–33, as many as 17·7% were blank and 18·6% of the total catches exceeded 20 crans. This is discussed further in the section on the Scottish fishery, page 256.

If now we consider the Shields 1931 figures, we see that the catches were much higher than in the following years in this area, or even in the Scottish fishery (i.e. considering the samples obtained by us). Only 1·5% of the catches were blank and 24·6% exceeded 20 crans. This condition is even more marked between the 1st July and the 15th August (the period characterised by marked losses) when the distribution of the catches is as follows :

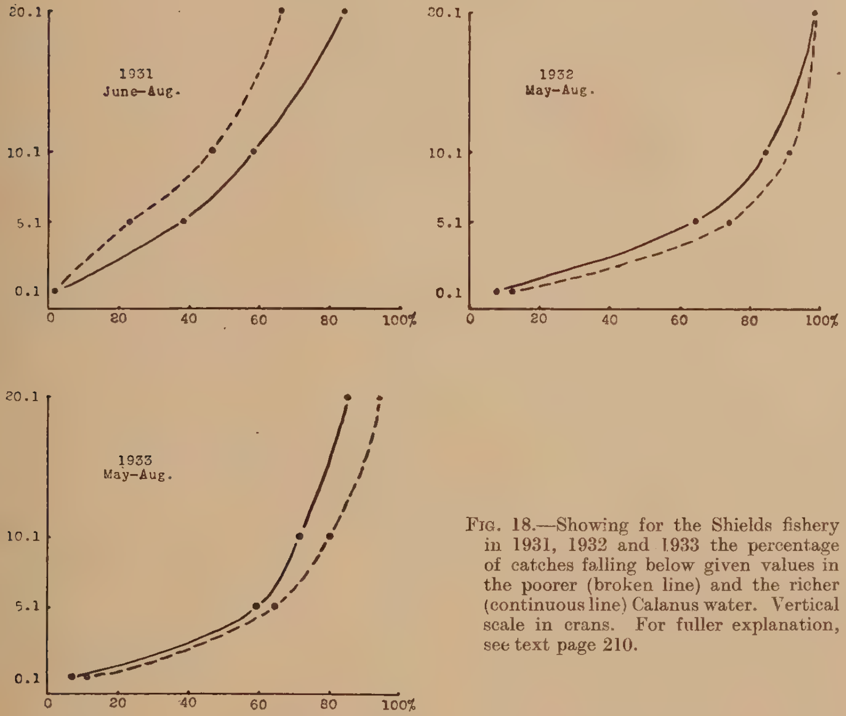

FIG. 18.—Showing for the Shields fishery in 1931, 1932 and 1933 the percentage of catches falling below given values in the poorer (broken line) and the richer (continuous line) Calanus water. Vertical scale in crans. For fuller explanation, see text page 210.

Herring catches range.	Percentage of total catches 1st July—15th August, 1931.
0·0 crans.	0·0
0·1–5·0 ,,	24·0
5·1–10·0 ,,	20·0
10·1–20·0 ,,	25·2
20·0 and over	30·8

The area fished during this period was relatively near the coast and must have contained a much denser concentration of herring than occurred usually on the east coast north of the Humber. No blank catches occurred, 56% of the catches were over 10 crans and 30·8% exceeded 20 crans. In particular at this time Calanus was relatively very scarce (see Table I).

TABLE V.

(For details, see text.)

Period and Year.	Theoretical percentage Gain or Loss to be obtained by avoiding the lowest quarter, half, two-thirds and three-quarters of the waters sampled.				Average of (a), (b) and (c).
	Lowest quarter. (a)	Lowest half. (b)	Lowest two-thirds.	Lowest three-quarters. (c)	
1–15 May, 1932	+25·3	+75·1	+33·0	+48·0	+49·5
,, 1933	+25·4	+11·8	−30·9	−10·5	+ 8·9
16–31 May, 1932	+18·0	+41·7	+61·4	+91·4	+50·4
,, 1933	−10·8	+19·1	+38·5	+17·6	+ 8·6
1–15 June, 1932	+ 1·1	+ 4·4	+ 3·2	+16·9	+ 7·5
,, 1933	+14·8	+16·2	− 8·4	−32·2	− 0·4
16–30 June, 1931	+ 8·3	+13·6	+61·0	+61·2	+27·7
,, 1932	− 3·5	+ 4·8	+ 8·1	+24·7	+ 8·7
,, 1933	+ 0·4	−12·6	+ 7·9	+22·8	+ 3·5
29 June–15 July, 1931	− 4·7	− 9·7	+ 3·1	+18·9	+ 1·5
1–20 July, 1932	+ 6·8	+20·3	− 7·0	− 6·3	+ 6·9
1–15 July, 1933	+ 3·7	+21·3	+11·0	−23·8	+ 0·4
16–31 July, 1931	−18·6	−29·9	−31·8	−41·0	−29·8
,, 1933	+16·0	+43·9	+68·8	+61·8	+40·6
1–15 Aug., 1931	−13·4	−40·3	−52·8	−61·9	−38·5
,, 1932	−41·2	−43·6	−39·8	−28·4	−37·7
,, 1933	+17·4	+39·7	+66·5	+96·3	+51·1
16 Aug.–8 Sept., 1931	+ 8·3	+ 3·1	+15·5	+32·2	+14·5
16–31 Aug., 1932	+11·0	+35·3	+22·4	+29·9	+25·4
16 Aug.–1 Sept., 1933	+11·1	+40·5	+83·3	+109·5	+53·7
Average all results	+ 3·8	+12·7	+15·7	+21·4	+12·6
Average excluding 1–15 Aug.	+ 6·6	+17·6	+19·9	+24·8	+16·3

It seems reasonable to suggest that these shoals did not consist of feeding fish, but of fish collected for spawning and moving about the area irrespective of the Calanus distribution (but see also page 223).

Now instead of dividing the series of samples in each period into two equal sets (half having the lower Calanus numbers and the other half having the higher ones), we can divide each series of samples into (*a*) the lower three-quarters and the higher quarter and (*b*) the lower quarter and the higher three-quarters. It is now possible to obtain two further series of percentage gains and losses showing the results to be expected if (*a*) the fishermen were able to find for each catch waters containing Calanus of a similar value to those in the top quarter of the series and (*b*) they were only fortunate enough to obtain waters similar in average Calanus content to those represented by the top three-quarters of the series. Table V shows these results (and also one based on correlating Calanus and herring in the bottom two-thirds and the top third of the series) together with those of the lower and higher halves, for comparison. It will be seen that on the whole, these results become higher as we pass from the avoidance of the bottom quarter, half, two-thirds and three-quarters

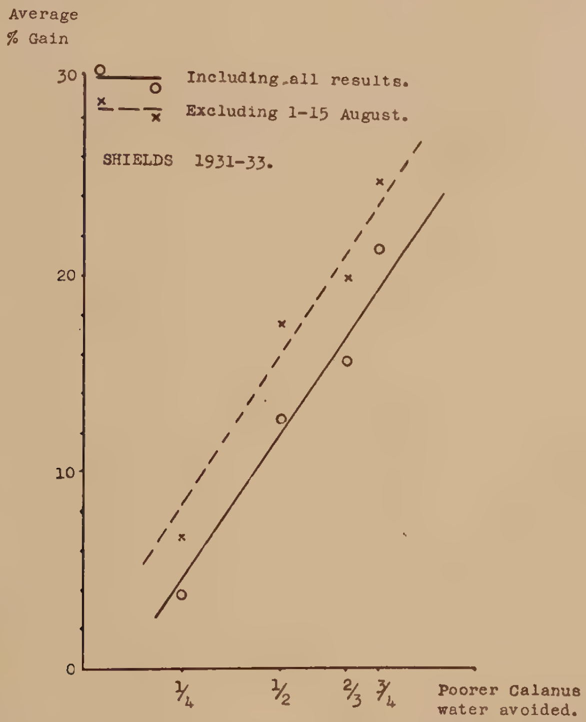

FIG. 19.—Showing the theoretical estimated average gains which might have been obtained by the Indicator boats had they avoided the poorer quarter, half, two-thirds or three-quarters of the Calanus waters in the Shields fishery, 1931–33. For fuller explanation, see text. Averages based on all results are shown as circles, and those based on all results except those for the first half of August are shown as crosses.

of the Calanus numbers. This is expressed most suitably by averaging each column: we thus find increasing gains of 3·8%, 12·7%, 15·7% and 21·4%: or if we exclude the period August 1st–August 15th, the gains are 6·6%, 17·6%, 19·9% and 24·8%.

These results are expressed in graphical form in Fig. 19, where it is seen that the points lie close to a straight line, a feature which would seem to be of considerable ecological interest. It is also of economic importance, for we see that over four ranges of Calanus values we can deduce an increasing gain in the catch based on aiming at an increasing density of Calanus, or, inversely, avoiding more and more of the water poor in Calanus. In other words, this means that not only in a broad way is the catch associated with the higher half of the Calanus samples larger than that with the lower half, but the correlation of which this is evidence extends further throughout the whole range of the Calanus samples on the average (not in all periods), and that if the fisherman aimed at a much higher value of Calanus, on this evidence he would make much higher gains*; but against this must be borne in mind the relative scarcity of the dense Calanus samples shown at the higher end of the table. If too high a value is aimed at he may well waste too much time and fuel trying to find suitable water, just as if the careless fisherman aims at a lower average he will usually find this easily, but gains, if any, will be proportionately lower.

In column 6 of Table V, the average of columns 2, 3 and 5 is shown. It seemed likely that the average of all these results would give an even better estimate of the potential value of the Indicator over the three years than that given on page 207, since it is based on estimates obtained from the same material under a more exhaustive analysis: the figure obtained, however, a gain of 12·6%, is almost identical with the previous one (12·7%).

The table also shows another and related feature, to which Prof. R. A. Fisher has kindly drawn our attention. If for each half-monthly table the ascending series of Calanus values is divided into four consecutive quarters, and the catches associated with each quarter are averaged, we can then obtain for each quarter an estimate of its mean catch as a percentage of the mean catch of the whole table. This has been done for each half-month and a mean percentage obtained for each quarter over the three years. The approximate results are as follows: First (lowest) quarter, 87%; second quarter, 86%; third quarter, 95% and the fourth (highest) quarter, 121%.† It would appear that the differences between the means of the catches associated with the lower two (and to some extent the third) quarters are of little significance, whereas the mean of the fourth quarter is significantly different from these three. On the whole the correlations must depend on the relatively high catches associated with the fourth quarter, i.e. the quarter containing the highest Calanus samples. This again would seem to be of considerable ecological and economic importance, and again emphasises the importance of the fishermen endeavouring to locate the richest Calanus water, even where this necessitates the expenditure of a little more fuel.

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* There is almost certainly a limit to this.

† It may be observed that these four figures do not total 400 as they should theoretically. This is due to certain approximations made in calculating the percentages for a table consisting of an odd number of samples.

As we saw on page 187 the Shields material can also be used on an Individual Boat basis. In all there have been seven such boats, here denoted by the letters A–G. The following table shows the number of periods and samples on which the results for each boat have been based, and the average estimated percentage gain.

Boat A	10 periods	156 tests	averaged 20·9% gain
,, B	5 ,,	64 ,,	,, 32·8% ,,
,, C	4 ,,	52 ,,	,, 9·9% ,,
,, D	6 ,,	92 ,,	,, 14·3% ,,
,, E	2 ,,	26 ,,	,, 13·8% ,,
,, F	3 ,,	47 ,,	,, 13·3% ,,
,, G	1 ,,	20 ,,	,, 33·9% ,,

Of the seven fishing boats, all show a gain over the total period of using the Indicator. With regard to Boat C, reference to page 189 shows that by considering the actual number of crans caught during the four periods, or the sum of the average catches during each period, one gains the impression that over the whole time an appreciable negative correlation resulted. The table above records in opposition an average gain of nearly 10%. This emphasises certain fundamental differences in the methods of obtaining results. Conclusions based upon the actual average catches for each period will give estimates of the probable gain or loss to the fishermen in crans of herring, but it will not give an idea of the probable monetary gain or loss through the season. On the whole the price of fish varies inversely with its abundance, and for this reason it is more satisfactory to base our ideas of the real value of the Indicator on the proportionate gain or loss, than on the actual gain or loss in crans (thus it is reasonable to suggest that the Boat C would have gained appreciably in time or money by using the plankton indications, although he might have obtained fewer herring).

The average gains and losses for the year as obtained from these Individual Boat results are different from those in which all the boats are massed together. The years 1931 and 1932 gave a higher average for the

Individual Boat data than for all the boats taken together, but in 1933 the average is slightly lower. Thus :

	1931.	1932.	1933.
Average % gain or loss averaging all boats	—12·6	+19·7	+22·5
Average % gain or loss averaging individual boats	— 0·5	+27·2	+20·8

It may be that the difference in 1931–32 is due to the fact that when dealing with the individual boats the differences in catching power of the boats and their methods and locations are not disturbing the results as they may be when the boats are combined. If this is so then the relative similarity shown in 1933 might be due to the boats having at least one more feature in common than in the earlier years : in this year they were already adopting the plankton indications as a guide to locating the herring.

The mean gain for the thirty-one individual boat periods over the three years is 19·3% as against 12·7% shown by the previous estimations for the " All Boat " results. The Standard Error is ±5·13% with a consequent value for " t " of 3·76.

By means of percentages it is possible to estimate more exactly the probable gains and losses obtained by using the Indicator. By averaging the percentages for each half-month (Table V. All boats, with Calanus divided into lower and higher halves) we find that off Shields high probable gains decrease from early May to the end of June, rising in the first half of July and then dropping to the end of the first half of August when there may be a substantial loss, followed by a gain in the period August 16th–31st. The order of the magnitude of these gains and losses is suggested in the following table :

Date.	May.		June.		July.		August.	
	1–15	16–31	1–15	16–30	1–15	16–31	1–15	16–31
Average % gain or loss	+43·5	+30·4	+10·3	+1·9	+10·6	+7·0	—14·7	+26·3

Our records in the Shields area end in early September (although the season may last into October).

Further information regarding the correlations and feeding habits off Shields in July and August is desirable, but at the present time it seems inadvisable to use the Indicator for positive correlations with Calanus during the first part of August.* On the whole, our information suggests the possibility that not only are the herring at this time not following Calanus, but that they may even be avoiding it and other food : further work may confirm this, but the series of positive correlations found in July and August in 1933 suggests very strongly that it will not be possible to formulate any general rule applicable to all years, and that in certain years (perhaps occurring in cycles) it may be possible to use the Indicator throughout the season. Further, since herring are fish which spawn on the sea bed and are known to prefer some types of bottom to others and to spawn in fairly definite places, it is possible that when the shoals assemble for spawning they will do so in relation to fixed geographical features, and

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* A number of Indicators were used commercially during 1934, 1395 and 1936, and this advice was given to the skippers of the boats using the instrument.

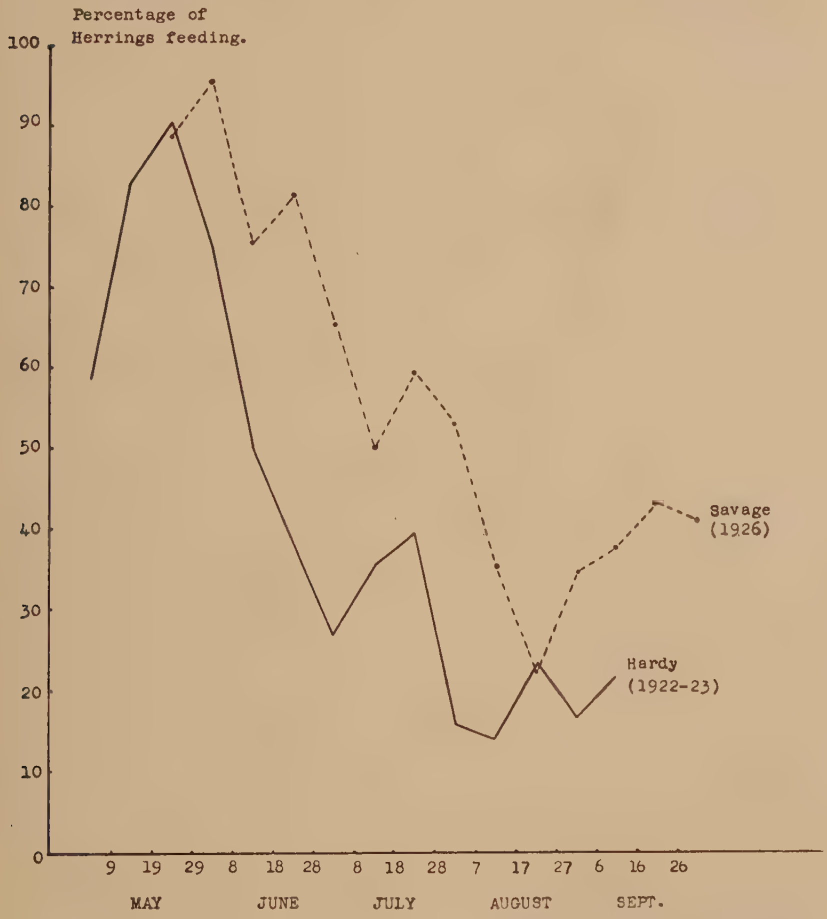

Fig. 20.—Showing the changes in the percentages of feeding herring in the Shields area for 1922–23 and 1926 as shown by Hardy (1924) and Savage (1931) respectively. See footnote on page 218.

that as a result, any correlation between the herring and Calanus will vary according to the apparently accidental presence or absence of Calanus in the waters over the spawning grounds and the correlations would be positive or negative accordingly. Again, if this were found to be correct, it would not be possible to formulate any general ruling for the use of the Indicator at this period.

CALANUS AND THE FEEDING OF THE HERRING.

The principle on which the Indicator work was based was that during the feeding season, herring would tend to follow the organisms on which they are feeding. During the late spring and summer the principal of these is *Calanus finmarchicus* (see Hardy, 1924 ; Savage, 1931 ; Jespersen, 1928). At times Calanus exceeds the other copepods in actual numbers in the stomach contents of the herring, but even when it is not so abundant, its large size compared with the other common species in the area suggests that it is still of great importance in the food. Now Hardy (1924) showed how the proportions of herring feeding in the Shields area increased rapidly in April to a maximum in May and then fell off towards the end of the season with a final spurt of feeding off Shields and the Yorkshire coast in September, followed by a period with little or no feeding, which condition also holds in the Yarmouth fishery until the end of the year.

In 1926, Savage (1931) found substantially similar results : these together with those of Hardy are shown graphically in Fig. 20.* It will be seen that the trend shown by these graphs is broadly similar to that of the average percentage Gains and Losses as shown by the Indicator over the three years 1931–33 (see p. 216 and Fig. 17). The prevalent gains in the early part of the season correspond with the high percentage feeding at that time : the " losses " or negative correlations in July and August correspond with the slackened feeding found by Hardy and Savage, and it seems possible that the positive correlations found in August off Shields and in September off the Humber would correspond with the spurt of feeding found for the same areas at the end of the season. From October onwards, the impossibility of correlation as brought out by the marked scarcity of Calanus, agrees with the almost entire absence of feeding found off Yarmouth at that time.

Thus there is a general agreement between the separate data found by different workers in this area, but the information for 1931–33 has interesting variations, both between the different years and within the years. It is important to obtain, if possible, some idea of the significance of these variations: Are they, as suggested on page 202, due to accidental variations in the efficiency of the instrument as a means of correlating herring and Calanus, or have they a different and more important significance? We are indebted to Mr. R. E. Savage, of the Ministry's Laboratory at Lowestoft, who has kindly placed at our disposal data, as yet unpublished, from his Shields herring stomach examinations in the years 1931–33. The relation between our results and Mr. Savage's can best be shown by means of a series of graphs. Table VI and Fig. 21 show a comparison of the numbers of Calanus found by Mr. Savage in herring stomachs for each 10-day period throughout the season, and the numbers of Calanus found by the Indicator in the plankton at a depth of 7–10 metres. There is a general agreement between these results. We see that on the whole when Calanus is more abundant at 7–10 metres it is eaten in greater quantity by the herring, and when it is scarce, usually little is found in the herring stomachs.[†] Table VI shows that the two aberrant points

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* Hardy's results have been re-graphed in ten-day periods from the figures in Savage's paper (1931, see p. 13). These results are recalculated from the data in Hardy's 1924 paper.

TABLE VI.

SHOWING THE NUMBERS OF *Calanus finmarchicus* PER 100 HERRING STOMACHS, IN 10-DAY PERIODS FOR THE SHIELDS AREA 1931–33,[*] TOGETHER WITH THE AVERAGE NUMBERS FOUND IN THE PLANKTON FOR THE SAME PERIODS.

10-day period ending.	Numbers of *Calanus finmarchicus* per 100 stomachs.			Numbers of *Calanus finmarchicus* in plankton.		
	1931.	1932.	1933.	1931.	1932.	1933.
29th April . .	73,387	—	166,200	—	—	470^{1}
9th May . .	128,012	1,423	36,114	—	321^{8}	824^{9}
19th May . .	85,442	10,759	24,939	—	244^{21}	366^{7}
29th May . .	46,740	27,005	20,686	—	415^{23}	199^{6}
8th June . .	55,717	24,708	6,861	41^{6}	800^{32}	49^{21}
18th June . .	12,646	14,645	15,997	—	896^{33}	336^{27}
28th June . .	26,463	37,321	18,111	99^{24}	$1{,}030^{32}$	276^{26}
8th July . .	5,540	16,292	22,790	84^{11}	265^{22}	$1{,}001^{18}$
18th July . .	12,741	2,927	11,912	36^{16}	183^{13}	$1{,}205^{20}$
28th July . .	255	11,603	31,134	69^{25}	114^{2}	372^{12}
7th August . .	2,010	1,601	5,703	115^{16}	380^{1}	91^{24}
17th August . .	2,913	1,492	3,273	89^{10}	185^{13}	56^{12}
27th August . .	6,479	2,444	5,947	59^{15}	109^{11}	40^{1}
6th September .	2,777	2,524	6,416	92^{9}	2^{6}	84^{8}
16th September .	3,953	251	13,978	24^{2}	—	—
26th September .	—	536	—	—	—	—
6th October . .	—	—	0	—	—	—

The index figures show the number of samples on which the average is based.

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[*] This information was kindly supplied by Mr. R. E. Savage of the Ministry of Agriculture and Fisheries.

[†] Seeing that Savage found such large numbers of Calanus in the herring stomachs in May, 1931, it seems likely that there must also have been a large number in the plankton, suggesting a much greater number than that found by the Indicator later in the year (see also p. 183).

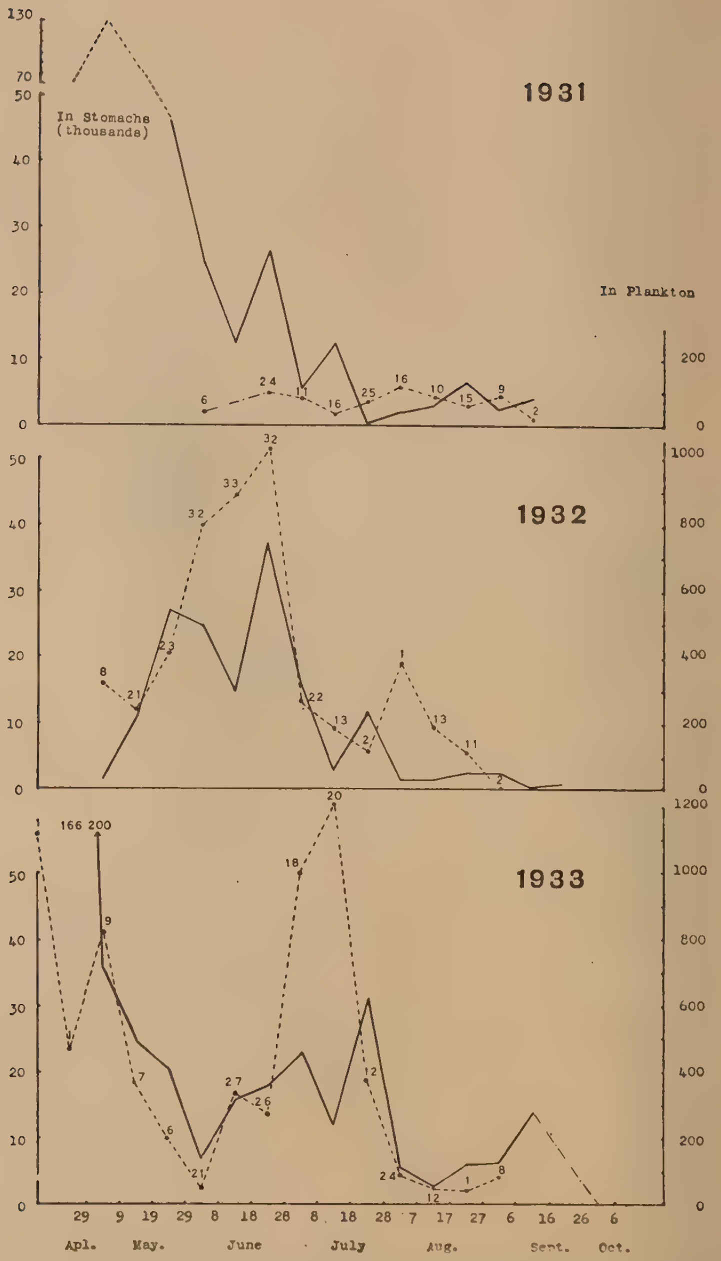

Fig. 21.—Showing the variations in the numbers of the available Calanus as found by the Indicator at 7–10 metres (Calanus per disc: broken line) and in the numbers eaten by the herring (Calanus per 100 herring stomachs: continuous line) for each ten-day period in the Shields fishery, 1931–33. The latter figures have been kindly supplied to us by Mr. R. E. Savage of the Ministry of Agriculture and Fisheries, from his as yet unpublished material.

in these graphs occur when two high feeding periods coincide with (1) a period in 1931 comprising only six plankton samples taken (by the R.S. *Onaway*) on one night and (2) a period in 1933 when only one sample was obtained. When we consider that the stomachs were not necessarily obtained at the same time and in the same places as the Indicator samples we could not expect a very marked correlation between the variations of each. The degree of correlation between the two factors is shown in Fig. 22 derived from Fig. 21 and Table VI. Regarding these graphs we may note further that in 1932 the period of most intensive feeding was a month later than in 1931, and in 1933 there was a second period of intensive feeding about three weeks later than in 1932.

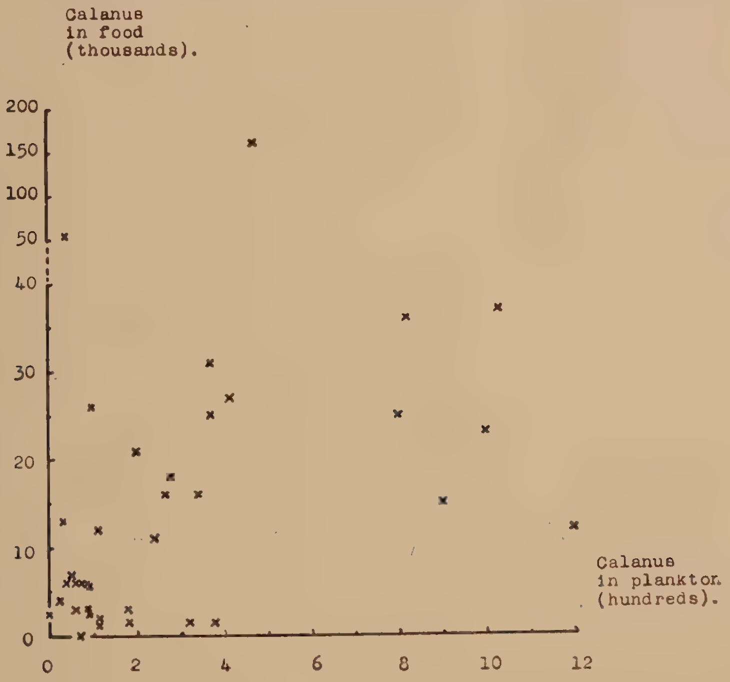

Fig. 22.—Showing for the Shields fishery, 1931–33, the relation between the intensity of feeding of the herring upon Calanus (as shown by the analyses of stomach contents) and the available supplies of Calanus at 7–10 metres (as found by the Indicator samples). The former figures have been kindly supplied to us by Mr. R. E. Savage of the Ministry of Agriculture and Fisheries, from his as yet unpublished material.

Now, Hodgson (1925) has shown that the usual course of the fishery at Shields is as follows: In April and early May catches are made of fish just recovering from the spring spawning; these are mainly four-year-olds and are succeeded by the typical fat Shields herring, which are small, only three years old, and in particular, virgin fish. They form an important part of the catch and appear to come mainly for feeding purposes. (Hodgson points out that there is usually an abundant zooplankton at this time.) They appear towards the end of May and are found to be growing up to the end of September. In July and August, these fish are displaced by the vanguard of the autumn-spawning herring, of which the main body supplies the autumn fishery in the Southern Bight. The Shields representatives of these herring are mainly four years old and about to spawn for the first time, though older fish may appear later. This generalised statement of events which we may imagine to vary within limits, is important in any consideration of the ecology, and in particular, the feeding relationships of the herring, since most observers are agreed that the herring cease to feed at spawning time (Hardy, 1924, and Savage, 1931, etc.). Giard (1903) and Brook and Calderwood (1885), however, suggest that the herring may feed hard immediately after spawning.

A possible explanation of the negative correlations found in July and August of 1931 and 1932, might be that they were caused by the presence of spawning fish in the shoals : if spawning herring do not feed then large catches might be taken irrespective of the distribution of the food : the second wave of positive association following on the negative one might be due to the feeding of post-spawning fish as suggested by Giard, etc. (loc. cit., above). We have no accurate information about the constitution of the herring shoals at these times, although reports in *The Fishing News* (see p. 205) suggest that spawning did occur about July in 1931 and in August in 1932, and moreover that in 1933 (when no negative correlations were found) spawning fish were not so evident as in the previous years and on the whole appeared even later.

Further, with regard to the variations in the individual years, it seems to be important to note that if Hardy's suggestion should be borne out that a crustacean diet may be necessary to the ripening of the gonads prior to spawning (Hardy, 1924, p. 18) certain differences over the three years in regard to the distribution of Calanus may be significant. Reference to Fig. 21 shows that in 1932, the season of maximum abundance of Calanus as shown by our plankton samples was probably a month later than in 1931* and that in 1933 whilst Calanus was abundant in April, there was a marked period of scarcity in late May and early June followed by a maximum in mid-July, i.e. some three weeks later than the maximum in 1932. If a period of intense feeding on crustacea should be necessary prior to spawning, it is possible that the late arrival of the Calanus in 1933, which probably covered a wider area of the North Sea than the relatively small one under consideration, may, indirectly, have been the cause of a later spawning in this area, i.e. it may have affected the stock of fish normally entering this area in order to spawn.

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* See also p. 183 and footnote on p. 219 referring to Mr. Savage's results.

It is interesting to note that (1) large numbers of Calanus were taken later each year, (2) the period in the fishery during which small herrings were caught was longer each successive year and (3) that in 1931, whilst there was a period of poor or negative correlation in July and August, in 1932 this was shorter and in 1933 high positive correlations were found at this time. It may be too speculative to suggest that the negative correlations in 1931 and 1932 were due to the presence of non-feeding, spawning herring and that the absence of negative correlations in August, 1933, was due to delayed spawning, but it is evident that some change did occur in the nature of the correlation in 1933 as compared with 1931 and 1932.

An alternative explanation might lie in the following consideration. A study of the histograms representing individual and average catches of herring together with the graphs of the associated numbers of Calanus, shown in Figs. 5, 7, 9, 11, 13 and 15, gives interesting information regarding the strengths of stock of both Calanus and the herring on the grounds during the three seasons and also suggests that there may be at times a reduction in the Calanus stock by the grazing action of the herring when present in very large numbers.* Turning to Fig. 7 (July and August, 1931) we see exceptionally large numbers of herring on the grounds and the Calanus stock has the appearance of being grazed very low. Judging by the numbers of Calanus found in the herring stomachs (figures kindly supplied by Mr. R. E. Savage)—see Fig. 21—we can see that in the earlier part of the season the herring were eating enormous numbers of Calanus, but subsequently the numbers found in the stomachs became very low. This fall in the numbers of Calanus in the stomachs coincides with the greatly increased numbers of herring taken in the fishery in June (see Fig. 16) and suggests that there were not enough Calanus on the grounds to feed so large a stock of fish. It may indeed be that the negative correlations found in July and August, 1931, were not necessarily due to the advent of non-feeding spawning herring, as has been suggested above, but to the presence of hungry herrings searching all over the area for Calanus to feed upon, and thus accounting for their widespread distribution in late July and early August. If the ratio of herring to Calanus is exceptionally large then the Calanus in the samples of plankton associated with the larger catches of herring may be small because the stock in the locality has been greatly reduced by the feeding of the latter.

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* That the stock of Calanus on the Shields grounds is intensively grazed, has been suggested by Savage in 1931.

Again in Fig. 15 we see that the herring on the grounds in July, 1933, presented a higher average than at any time in the three seasons other than July and August, 1931. Looking at the curves of the Calanus numbers we see a gradual reduction passing from the first half of July, 1933, to the second half of August. The number of herrings on the grounds also diminished in August, but it was still fairly high in the first half. The herring-Calanus ratio as a whole was lower than in 1931, and positive correlations held over the two months. In most other periods the quantities of herrings are not so large and the curves of Calanus show that its stock was not reduced to a low level over the whole area, regions of richer Calanus remaining in parts, and in these periods the herring-Calanus correlations were mainly positive.

These diagrams do suggest the possibility that the herring can seriously reduce the Calanus stock by grazing, and that if the herring-Calanus ratio is very high (as in late 1931) a positive feeding relationship between the two forms might appear as a negative correlation owing to the extensive reduction of the prey (Calanus) in those localities where the predators (the herring) are most abundant. The negative correlation in early August, 1932, might also be explained thus, the herring-Calanus ratio being high but against this we must consider the following point. Although the reduction in the Calanus stock in early July, 1932 (Fig. 11), is as marked as that in early August, 1933 (Fig. 15), yet the stock of herring on the grounds in 1932 was nothing like so strong as that which might possibly be held to have brought about such a reduction in 1933. If the marked reduction in the Calanus stock in 1932 cannot reasonably be attributed to the grazing of the herring we must be prepared to recognise that the low numbers of Calanus in 1931 and late 1933 may also be due (at least in part) to other reasons. With the inadequate information at our disposal we can go no further: whatever may be our explanation, we must remember that both analyses of the shoals of herring and correlations between the herring and the plankton in this experiment are subject to the movements of the fishing fleet which may produce apparent variation in the constitution of the shoals of fish and also of the plankton.

Seasonal Differences and Hydrological Considerations.

It is worthy of note that other changes have occurred in this area over the three years 1931–33, and it may be that these also can be associated with those previously mentioned. We have already (p. 186) shown that the numbers of Calanus during the fishing season seem to have been increasing during the three years,* whereas the numbers of the other copepoda on the whole decreased. On page 222 we saw that the periods of maximum abundance of Calanus extended later each year, likewise (as shown by Mr. Savage's figures) the period of most intensive feeding on Calanus (p. 220). In the Shields area (p. 232) the amount of phytoplankton decreased from 1932 to 1933, whilst in the Southern Bight it has been increasing in bulk each year (see Savage and Hardy, 1935, and Hardy in collaboration with Henderson, Lucas and Fraser, 1935). Limacina (see Table on p. 227) was progressively scarcer each year during the period of observations,* although it attained higher maxima at the end of the season in 1931 and 1933 than it did in 1932 (p. 236). Herring catches in the vicinity of Shields decreased on the whole (p. 205) and as far as we have information available (see p. 205) it appears that the period when small unripe fish were to be caught extended later each year in these waters. The period of marked negative correlation between Calanus and the herring (see Indicator results, p. 182), so evident in July and early August in 1931, was less extensive in 1932 and in 1933 during the corresponding period the correlations were markedly positive. Reference to the Hydrological Bulletin for 1927–33 (1928–34) shows that on the whole in the centre of the Shields area, temperatures and salinities have been increasing since 1927–28.† For the northern North Sea, Tait (1935) has shown how the salinities have been increasing markedly during recent years, culminating (as far as information is up to date) in the year 1934.

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* It is perhaps also of interest to note that our records (see Part III) suggest that in the waters off the East Coast of Scotland, the numbers of Calanus increased markedly over the three years, and, to a lesser extent, those of Limacina also.

It seems likely that all these factors are not entirely unconnected and it may not be unreasonable to suggest further a connection with the Atlantic inflow which is known to have been increasing steadily over that time. The Report of the Ministry of Agriculture and Fisheries for 1933 (1934, section on Hydrography) shows how the easterly component of the Channel inflow through the Dover Straits has decreased steadily since 1930. This " is to be ascribed to an extra strong southward push of the waters from the north." " Only throughout January was there an inflow from the Channel anything approaching a bold stream." The recovery of drift bottles, liberated in Scotland in 1933, on the Suffolk coast also points to a very strong Atlantic inflow in 1933 round the north coast of Scotland (Scottish Fishery Board Reports, 1934). Russell (1935a) has reviewed past information concerning the value of certain plankton animals as indicators of unusual water currents and with reference to the increasing strength of the Atlantic inflow into the North Sea in these years it is interesting to note a number of instances of unusual organisms penetrating into the North Sea during that time.

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* See footnote on p. 224.

† Information from the Meteorological Office Records for Shields (1931–33) for these years shows that higher maximum atmospheric temperatures were attained each year and that the period of maximum temperature persisted later, i.e. for a longer time, each successive year.

In September, 1933, we found *Dolioletta gegenbauri* (Uljanin) apparently moving southwards in the North Sea in the latitude of Aberdeen (Lucas, 1933).* It seems possible that some of the doliolids which have been found by the Scottish Fishery Board to be penetrating further into the North Sea from 1928–33, are the same form (Scottish Fishery Board Reports, 1929–34). Kramp (1934) refers to the unusual occurrence of *Rhizostoma octopus* and *Chrysaora hysoscella* in Danish waters in 1933 (see also the finding of *Clione limacina, Limacina helicina* and *Sepia officinalis* referred to by Kramp, loc cit.). In addition to doliolids the reports of the Scottish Fishery Board for 1930–33 refer to other unusual organisms entering the North Sea during these years. Chief amongst these are: Larval Wrasse (*Ctenolabrus rupestris*) in September, 1930, and *Ommatostrephes sagittatus* on the Shetland herring grounds in 1930 and 1931 together with unusually large numbers of medusæ as Laodicea, Tiaropsis, Cosmetira, Mitrocoma and Obelia species in 1931 (see also Lucas and Henderson, 1936). *Cyclosalpa bakeri* in November, 1932, and the floating barnacle, *Lepas fascicularis* in July 1933, were also recorded off the Bressay Shoal.

Russell (1935b) has shown that many of these forms, with others, may be considered when present in the North Sea to be indicators of the presence of Atlantic water. In another paper (1935a) he demonstrated how the fluctuating movements of *Sagitta elegans* and *Sagitta setosa* since 1930 in the waters off Plymouth also demonstrated the gradually increasing strength of the Atlantic pulse in the north during those years: the predominance of the *Sagitta elegans* in 1930 gave place to a dominance of *Sagitta setosa* late in 1931. From 1930 to 1934 the proportionate dominance of *Sagitta setosa* at Plymouth on the whole tends to agree with the abundance of *Rhizosolenia styliformis* (also an indicator of Atlantic water) in the Dogger Bank region. The abundance of both increased from 1930 to 1933 and both seem to have been rather less abundant in 1934.

It is thought important to note, where possible, broad changes of the above nature which may be associated over a term of years, and which apparently include such diverse planktonic forms as copepods, doliolids, pteropods and the phytoplankton, the pelagic herring and the physical conditions of the environment, whilst there are probably many other factors which we are not at present able to enumerate. We have noted what seem to be important changes in the Shields herring fishery during the years under review and we must consider the possibility that these changes (and other similar changes in fisheries in these waters) may be a reflection of more general changes occurring in the North Sea as a whole.

The Limacina-Herring Correlations.

Whilst in 1931, both for the Scottish and Shields areas, we considered that we had good evidence of a negative correlation between Limacina and the herring, we had later to qualify this view. Our first results were based upon a table combining all the results then available, without any regard being paid to variations within the season. In the Shields area for the three years 1931–33 we have the following average catches of herring (in crans) for different ranges of Limacina.

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* Young *Luidia sarsi* (echinoderm larvæ) were also found in these waters during the same period.

	1931.	1932.	1933.	1931–33.
Limacina 0–99 .	$18{\cdot}89^{50}$*	$3{\cdot}98^{185}$	$8{\cdot}21^{170}$	$7{\cdot}59^{405}$
,, 100–249 .	$14{\cdot}26^{21}$	$4{\cdot}68^{19}$	$4{\cdot}94^{12}$	$8{\cdot}61^{52}$
,, 250–499 .	$9{\cdot}84^{16}$	$12{\cdot}09^{11}$	$3{\cdot}86^{4}$	$9{\cdot}85^{31}$
,, 500–999 .	$8{\cdot}93^{9}$	$3{\cdot}33^{3}$	$10{\cdot}08^{3}$	$8{\cdot}05^{15}$
,, 1,000 and over	$5{\cdot}19^{8}$	$2{\cdot}75^{1}$	$1{\cdot}00^{4}$	$3{\cdot}71^{13}$

In this table we see that whereas 1931 showed a marked negative correlation as a whole, 1932 showed an optimum catch in the region of 250–499 Limacina and 1933, although showing an optimum (almost certainly not significant) at 500–999, is on the whole more similar to 1931 than 1932. We might also note at this stage that whereas in 1931 52% of the samples showed concentrations of more than 100 Limacina, in 1932 and 1933 the numbers of such samples were much lower ; this is due partly to the fact that we have no samples before June 29th in 1931, whereas in the other years we have samples from early May onwards, and at these times Limacina was scarce, but there is also a significant difference in the numbers of Limacina appearing after June in the three years in this area. This is best shown by considering the percentage of samples with more than 100 Limacina from the end of June, together with the average catches of herring for the different ranges of Limacina from this date (including one sample on June 29th, 1931). In this way we find :

	1931.	1932.	1933.	1931–33.
Limacina 0–99 .	$18{\cdot}89^{50}$*	$4{\cdot}7^{42}$	$11{\cdot}9^{72}$	$12{\cdot}2^{164}$
,, 100–249 .	$14{\cdot}26^{21}$	$5{\cdot}8^{9}$	$6{\cdot}5^{7}$	$10{\cdot}7^{37}$
,, 250–499 .	$9{\cdot}84^{16}$	$12{\cdot}9^{9}$	$5{\cdot}0^{3}$	$10{\cdot}3^{28}$
,, 500–999 .	$8{\cdot}93^{9}$	$3{\cdot}3^{3}$	$10{\cdot}1^{3}$	$8{\cdot}1^{15}$
,, 1,000 and over	$5{\cdot}19^{8}$	$2{\cdot}8^{1}$	$1{\cdot}0^{4}$	$3{\cdot}7^{13}$
Percentage greater than 100	52%	34%	19%	

On the whole very similar results are obtained, but there is this difference that although in 1933 Limacina attains at the end of the season a higher average than throughout 1932 (see p. 236), yet throughout the period for which we have samples, the percentage with more than 100 Limacina is less than in the two previous years, in fact the percentage decreases steadily from 1931 to 1933, so that during the fishing season its effects (whether good or bad) might be expected to decrease, since the area of water in which it was abundant became less and less. If we consider the correlation over the three years we find an almost perfect negative relationship after June, whereas, including all results from May onwards, the relationship was of a different type, the maximum average being associated with 250–499 Limacina. This demonstrates well the unsatisfactory nature of correlating results without reference to variation during the passage of time. The catches in May and June of 1932 and 1933 were low, and were associated with a low Limacina population, thus affecting the general correlation. The ecologist must always be prepared to distinguish between correlations in time and in space. Organisms which may be correlated positively in time (their numbers rising and falling similarly during a season), may yet be negatively associated in space, and *vice versa* : perhaps this has particular application in pelagic ecology, in which all the forms are not only liable to sudden fluctuations in actual numbers, but also to sudden migrations, both active and passive.

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* The indices denote the number of samples.

TABLE VII.

Showing the Average Catches of Herring in Crans corresponding to Lower and Higher Limacina Numbers. The Higher of the Two Catches is shown in Heavy Type.

Year.	Area.	Period.	Average catch with Limacina 0–99.	Average catch with Limacina 100 and over.	Sign of Correlation.
1931	Shields	29 June–15 July	$17{\cdot}6^{20}$	$\mathbf{27{\cdot}0}^{1}$	+
,,	,,	16–31 July	$\mathbf{23{\cdot}6}^{21}$	$13{\cdot}2^{16}$	—
,,	,,	1–15 August	$10{\cdot}5^{4}$	$\mathbf{12{\cdot}2}^{13}$	+
,,	,,	16 Aug.–8 Sept.	$\mathbf{11{\cdot}2}^{5}$	$7{\cdot}6^{24}$	—
,,	Humber	1–30 Sept.	$\mathbf{26{\cdot}7}^{6}$	$17{\cdot}4^{10}$	—
,,	,,	1–31 Oct.	$16{\cdot}0^{6}$	$\mathbf{102{\cdot}0}^{1}$	+
,,	Yarmouth	1 Sept.–31 Oct.	$\mathbf{19{\cdot}3}^{25}$	$13{\cdot}5^{1}$	—
1932	Shields	1–15 June	$\mathbf{4{\cdot}1}^{49}$	$3{\cdot}0^{1}$	—
,,	,,	16–30 June	$4{\cdot}3^{34}$	$\mathbf{4{\cdot}6}^{11}$	+
,,	,,	1–20 July	$4{\cdot}2^{20}$	$\mathbf{6{\cdot}2}^{12}$	+
,,	,,	1–15 Aug.	$5{\cdot}3^{3}$	$\mathbf{12{\cdot}4}^{8}$	+
,,	,,	16–31 Aug.	$\mathbf{4{\cdot}9}^{15}$	$3{\cdot}5^{2}$	—
1933	,,	1–15 June	$\mathbf{2{\cdot}1}^{37}$	$2{\cdot}0^{3}$	—
,,	,,	16–30 June	$\mathbf{9{\cdot}0}^{35}$	$2{\cdot}7^{3}$	—
,,	,,	16–31 July	$\mathbf{14{\cdot}0}^{18}$	$11{\cdot}1^{7}$	—
,,	,,	1–15 Aug.	$\mathbf{8{\cdot}0}^{26}$	$4{\cdot}3^{2}$	—
,,	,,	16 Aug.–1 Sept.	$0{\cdot}5^{3}$	$\mathbf{1{\cdot}1}^{8}$	+
,,	Humber	1–31 Sept.	$\mathbf{18{\cdot}6}^{8}$	$0{\cdot}3^{1}$	—

The indices denote the number of catches on which the average is based.

If now we examine the results in half-monthly periods corresponding to those used in the Calanus section, we find a considerable amount of variation. Table VII shows the correlations obtained by comparing the average catches associated with samples of less than 100 and more than 100, respectively. For the Shields area in May, 1932, and in May and the first half of July, 1933, no correlations are possible : also in 1931 there are no analyses of Limacina corresponding to the Calanus material from the R.S. *Onaway*. Of the remaining groups, eight are negative and six are positive, and whilst the 1931 and 1933 groups are mainly negative, those in 1932 are mainly positive. Such information as we are able to obtain from the Humber and Yarmouth areas is equally unsatisfactory: the data for both these areas is shown in Table VII.

We may now consider for the Shields area the progress of the fishery and the samples of Limacina through the season, and we see that in 1931 and 1933, as Limacina increases the catches decrease, whereas in 1932 the rise and fall of the catches and Limacina coincide very well (see Figs. 16 and 24). I think that this last factor is important; the negative correlations between Limacina and the herring in 1931 and 1933 may have been due to associations in time, as may also the positive correlation in 1932. Such an association may or may not be significant; we have not sufficient information to test this effectively. It is well known that herring will feed on Limacina (Hjort, 1912; Hardy, 1924; Savage, 1931) sometimes so much as to cram their stomachs and produce in cured fish the well-known condition of "black gut." Mr. Savage, of the Ministry of Fisheries Laboratory, Lowestoft, has kindly supplied us with the details of the feeding of herring on Limacina at Shields in 1931; a comparison

TABLE VIII.

SHOWING THE NUMBERS OF LIMACINA PER 100 HERRING STOMACHS* COMPARED WITH THE NUMBERS FOUND IN THE PLANKTON, IN 10-DAY PERIODS, IN THE SHIELDS AREA, 1931 AND 1932.

10-day period ending.	Numbers of Limacina per 100 stomachs. 1931.	Numbers of Limacina per 100 stomachs. 1932.	Numbers of Limacina in the plankton. 1931.	Numbers of Limacina in the plankton. 1932.
9th May	—	83	—	2^{8}
19th May	—	38	—	1^{21}
29th May	—	0	—	3^{23}
8th June	—	0	—	5^{32}
18th June	—	0	—	22^{33}
28th June	—	32	—	72^{32}
8th July	100	48	9^{11}	79^{22}
18th July	0	0	41^{16}	125^{13}
28th July	0	54	118^{25}	23^{2}
7th August	2,696	0	293^{16}	225^{1}
17th August	2,346	13	186^{11}	339^{13}
27th August	4,441	27	507^{14}	53^{11}
6th September	8,795	29	$1{,}341^{9}$	2^{6}
16th September	24,884	95	$1{,}980^{2}$	—

The index figures denote the number of samples on which the plankton averages are based.

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* These figures have been kindly supplied by Mr. R. E. Savage of the Ministry of Agriculture and Fisheries.

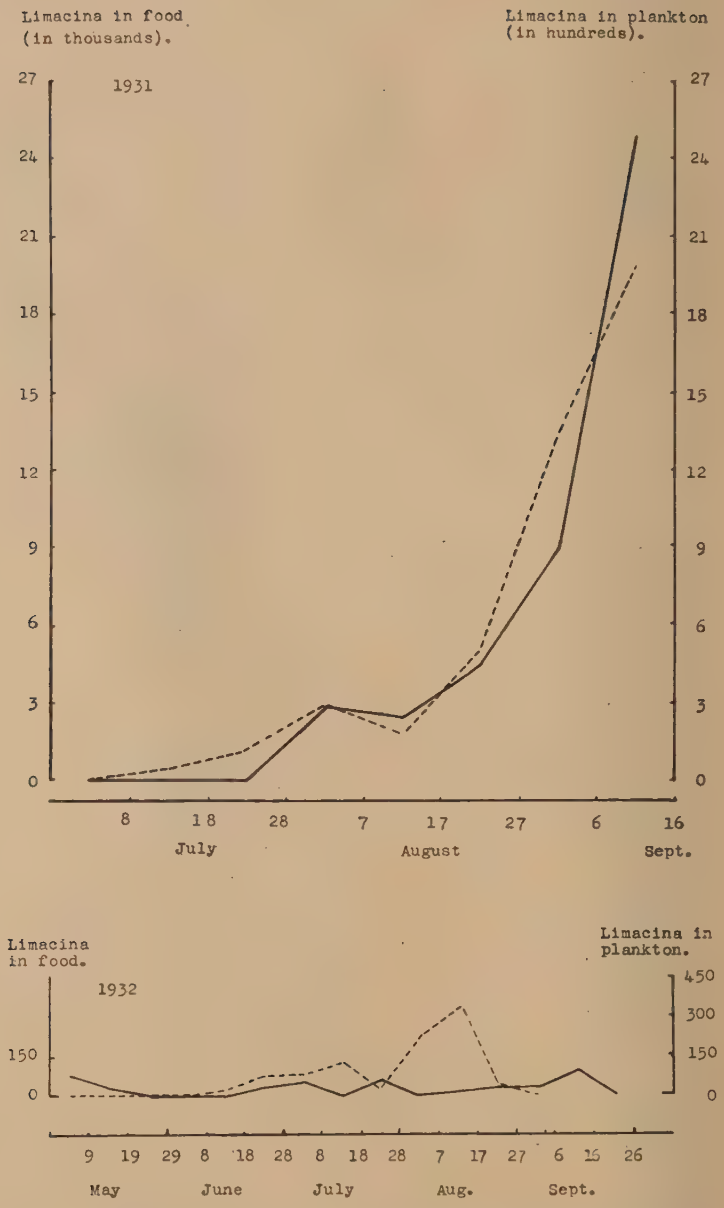

Fig. 23.—Showing the sequence of Limacina in the plankton (numbers per disc: broken line) and that in the food of the herring (numbers per 100 stomachs: continuous line) during ten-day periods in 1931 and 1932. It should be noted that the horizontal scale differs in the two years. We are indebted to Mr. R. E. Savage, of the Ministry of Agriculture and Fisheries, Lowestoft, who kindly supplied to us his as yet unpublished data relating to the feeding of the herring during these three years.

of the increase of feeding on Limacina with the increase of the organism in the plankton (sampled by our Indicator) is shown in Table VIII and Fig. 23 (1931). There is such a remarkedly close relationship between the two graphs that it is difficult to resist surprise that we do not find a marked positive relation between Limacina and herring during such times as it is reasonably abundant. In 1932 (see Fig. 23) Limacina was much scarcer in the plankton and Mr. Savage found very little of it in the food and no significant seasonal variation in the quantity. Yet we saw that in 1931 the correlation was mainly negative, whilst in 1932 it was mainly positive. We cannot at present account for these discrepancies, and although it is possible that normally the association between the herring and Limacina would be based upon a positive feeding relationship, there may yet be a negative association between the herring and dense concentrations of Limacina due to the avoidance by the herring of some at present unknown factors associated with large quantities of the latter. It must of course be borne in mind that the negative correlations in 1931 may well be due to similar factors to those producing the negative correlations between the herring and Calanus, although the abundance of Limacina occurred later in the season than the periods of negative correlation with Calanus. It is worthy of note here that there appears to be no association, either negative or positive, between the distribution of Calanus and that of Limacina: they may at times occur together in large numbers and at others they may be most abundant in different parts of the area.

It is clear that considerably more information is required, not only in regard to correlations between Limacina and herring, but also concerning the physiology of both organisms. It would be interesting to know, for instance, what is the actual food value of Limacina to the herring. The fact that large numbers are sometimes found in the stomachs does not necessarily imply that it is of high value to the herring as food. The difficulty of curing fish with "black-gut" suggests the inability of the herring to digest Limacina. Whatever may be the result of such researches, it seems evident that at present Limacina cannot be used as an indicator of herring catches, but it may be that further investigation with the Indicator will show that when Limacina is very abundant poor catches may be expected, especially if it is widely distributed. Results during 1930–33 from the Scottish and Irish areas also suggests this possibility. The average catch for all discs having over 500 Limacina is 4·94 crans (117 samples), and that for discs with over 1000 is 4·37 crans (70 samples), whilst the average for discs with less than 500 Limacina is 9·97 crans (1109 samples). Although this is not borne out area by area and period by period in detail, the consensus of results does suggest a negative effect on the size of the catches associated with *large* numbers of Limacina.

Notes on the Plankton taken with the Indicator off the East Coast of England.

Shields Area.

In the introductory paper two important factors are mentioned which qualify the value of the plankton material collected : (1) the Indicator hauls were horizontal and limited to a depth of 7–10 metres and (2) it is likely that considerable variation in the quantity of the plankton at this level may be due to the changes in its vertical distribution from time to time. In the plankton-herring correlations discussed in the foregoing pages these qualifications, whilst being kept in mind, need not be allowed to weigh too heavily : the correlations are found by using the Indicator in this particular manner and they appear in spite of the limitations of the method. In attempting to study the ecology of the plankton from this material it is necessary to give full weight to these factors.

Whilst the value of the material is limited in this way, with regard to certain organisms it is quite extensive. In the Shields area 545 samples have been taken, spaced fairly regularly in time over two and a half fishing seasons. In addition there is the advantage that all were collected in the fishing area, whilst fishing was in operation. For this reason notes on the more salient changes in the plankton over the period of investigation may be of value in supplementing the work of previous investigators and perhaps for reference in relation to future work.

Our work in this area, it will be remembered, began on the 29th June, 1931, and extended to the 8th September of that year ; in 1932 it extended from early May to the 1st September with a gap from the 21st July to the 6th August, and in 1933 we obtained samples in an almost complete series from the 29th April (there was also one sample on the 13th April) to the 1st September. In 1931 the samples were completely analysed, but in the following years, as already mentioned, the zooplankton analyses were limited to *Calanus finmarchicus*, total Copepoda and Limacina together with notes on the abundance of other organisms.* Table IX gives the numbers of these forms week by week together with those of the Dinoflagellates. The sequence of the variations is shown in Fig. 24 in graphical form. The chief points of interest arising out of these tables may be summarised as follows :

Diatoms and Phæocystis. There were no records in 1931 for the early part of the season, but 1932 and 1933 were characterised by the abundance of phytoplankton in May and early June. It seems probable that 1932 produced the greater concentrations of diatoms,

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* For part of 1932 there are also analyses of Temora, the Cladocera, Sagitta and other forms.

TABLE IX.

SHOWING THE AVERAGE NUMBERS OF VARIOUS PLANKTON ORGANISMS PER QUARTER MONTH IN THE SHIELDS AREA.

Month.	May.				June.				July.				August.				Sept.
Quarter.*	1.	2.	3.	4.	1.	2.	3.	4.	1.	2.	3.	4.	1.	2.	3.	4.	1.
Number of samples.																	
1931					6	—	5	19	9	12	18	19	10	7	13	9	7
1932	7	9	24	19	23	27	25	20	15	13	4	—	—	11	8	9	4
1933	5	7	5	6	16	24	18	20	12	13	11	14	18	10	2	7	2
Dinoflagellates, in thousands.																	
1931									2	7	5	29	36	45	65	39	39
1932	14	14	7	10	10	3	3	5	5	7		—	—	8	8	10	
1933	1	0	0	2	1	3	4	8	2	4	6	13	13	16	18		
Calanus finmarchicus.																	
1931					41	—	117	94	99	39	19	130	90	98	66	77	59
1932	290	72	270	731	749	962	965	845	205	175		—	—	175	194	39	
1933	961	422	249	104	41	306	195	564	1,030	1,015	1,077	293	74	66	67		
Copepoda other than Calanus.																	
1931									3,454	2,546	1,813	1,652	875	1,045	1,621	1,061	1,264
1932	506	492	505	990	1,346	1,320	2,143	938	1,421	1,107		—	—	697	963	596	
1933	321	267	37	146	180	1,134	1,221	975	1,125	1,274	745	852	841	885	699		
Limacina.																	
1931									5	28	106	163	292	235	232	851	1,659
1932	2	2	1	5	4	26	35	101	75	100		—	—	365	101	32	
1933	10	13	0	9	2	32	20	35	16	33	18	149	19	236	810		

* The numbers 1, 2, 3 and 4 represent the periods 1st–7th day, 8th–15th day, 16th–22nd day and 23rd day to the end of the month in question.

two-thirds of the discs obtained in the first part of May being coloured green. The chief forms were *Nitzschia closterium*, Chætoceros species and Thallassiosira spp. with local concentrations of *Rhizosolenia styliformis* and the flagellate Phæocystis. Fish were scarce at this time even compared with the general low average for the year. In 1933 there are two records of dense phytoplankton off Shields (i.e. two discs deeply coloured green by the diatoms), although less dense associations were frequent during early May and early June, but not in the second half of May: the principal forms were Thallasiosira and Chætoceros species and *Rh. hebetata*. The phytoplankton will be further considered in relation to the herring in Part IV of this series of papers.

TABLE X.

Showing the Average Numbers of Plankton Organisms per Quarter Month in the Shields Area, 1931.

Month	July.				August.				Sept.
Quarter*	1.	2.	3.	4.	1.	2.	3.	4.	1.
No. of samples	9	12	18	19	10	7	13	9	7
Dinoflagellates in thousands	2	7	5	29	36	45	65	39	39
Sagitta . .	1	5	15	13	9	7	32	57	23
Podon . .	60	38	31	19	9	1	1	0	7
Evadne . .	342	54	3	0	2	0	0	0	3
Calanus . .	99	39	19	130	90	98	66	77	59
Paracalanus and Pseudocalanus	652	310	170	271	115	57	280	260	276
Centropages .	204	523	441	361	177	247	153	175	147
Temora . .	137	191	126	279	68	225	549	130	230
Acartia . .	1,117	1,064	638	492	342	400	579	474	572
Oithona . .	556	165	188	106	32	33	28	21	32
Total Copepoda	3,553	2,585	1,832	1,782	965	1,143	1,687	1,138	1,323
Limacina .	5	28	106	163	292	235	232	851	1,659
Lamellibranch Larvæ . .	93	642	916	385	57	1	30	31	14

Dinoflagellates. In our samples these are mainly Ceratium species,† due probably to the differential catching power of the 60-mesh silk used on the discs. The year 1931 was easily the dominant year, an average of over 60,000 being found in August. In 1932 and 1933 the average figures were similar on the whole, but whereas the highest numbers in 1933 were towards the end of the season (as in 1931), in 1932 they were obtained in May with a secondary maximum occurring in August. An average of 27,000 in September, 1933, is the highest found in the two years.

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* The numbers are used as in Table IX.

† The evidence from 1931 suggests that in August and particularly in September, Peridinium and Dinophysis increase in abundance relatively and actually.

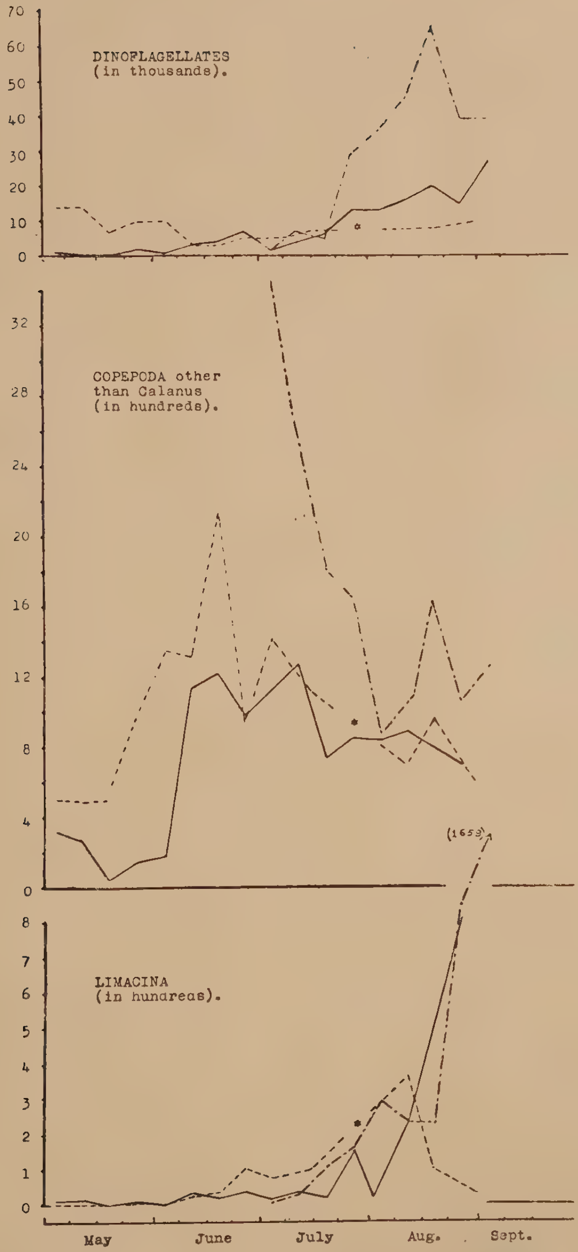

FIG. 24.—Showing the seasonal variations in the numbers of Dinoflagellates, Copepoda other than Calanus, and Limacina in the Shields area during the years 1931–33. (1931 :—dots and dashes; 1932 :—broken line; 1933 :—continuous line). * indicates a gap in the otherwise continuous series of observations for 1932.

Copepoda. The seasonal distribution of Calanus has already been described (see pp. 183–186) and Figs. 6, 8, 10, 12 and 14 show its spatial distribution at 7–10 metres, in consecutive half-months together with that of the herring. The distribution in time of the other copepoda is not dissimilar from that of Calanus in 1932 and 1933, but in 1931, whereas Calanus is scarce throughout the period of our results, at the beginning of that period the other Copepoda were very numerous, more numerous, in fact, than on any other occasion in the three years. How long this abundance lasted, unfortunately we cannot say. On the whole a broad similarity can be detected, a period of Calanus abundance in each year being followed by a scarcity ; the other copepods were abundant at the same time in 1932 and 1933, and then followed a drop in the numbers which was however very small compared with the drop in the Calanus population.

From the end of June onwards in 1931 we have the records of the numbers of the different copepods (see Table X). In early July, Acartia, Paracalanus and Oithona were very numerous : as the numbers of these forms decreased, Temora and *Centropages hamatus* became the chief features of the copepod fauna, although Paracalanus and Acartia had a small secondary maximum at the end of August. In 1932, Temora appeared to be very abundant during the first half of July, but the number of samples analysed for Temora in 1932 is not very large.

Cladocera. In 1931 the Cladocera as a whole decreased rapidly from the end of June, Evadne being more abundant at first and later Podon being the dominant form, although latterly the numbers of both were very low. In 1932 the maximum period occurred during the first half of June. Cladocera were not counted in 1933, but notes of their abundance were kept and these suggest a maximum density in late June.

Echinoderm Larvæ. In late June and early July an interesting feature was the appearance of large numbers of brightly coloured Echinoplutei. These were found both in 1932 and 1933 in large numbers, and to some extent in 1931, but not so numerous during the period of observation (from the end of June onwards). When these forms were abundant, the discs presented a brick-red appearance.

Limacina. The distribution of Limacina has been dealt with on page 227 ; 1931 was undoubtedly the year of its maximum abundance, but while under the period of observation it appears to have been scarcer in 1933 than in 1932, there were signs in 1933 that it was increasing and that it might attain a much greater density at the end of August and in early September than had been found at any part of the season in 1932.

TABLE XI.

Showing the Average Numbers of Various Plankton Organisms in the Humber and East Anglian Area, 1931–33.

1. *In the Humber Area*, 1931–33.

	1931.				1932.				1933.		
	Sept.	Oct.	Nov.	Dec.	Sept.	Oct.	Nov.	Dec.	Sept.	Oct.	Nov.
Dinoflagellates in thousands .	10	3	0	0	1	0	0	0	2	1	–
Calanus	12	36	1	0	18	10	0	10	31	11	–
Copepods other than Calanus	1027	1084	105	11	1040	1290	60	100	825	405	–
Limacina	348	457	1	0	26	0	0	0	30	10	–
Number of samples . .	16	7	6	6	6	1	1	2	9	2	–

2. *In the East Anglian Area*, 1931–33.

	1931.				1932.				1933.		
	Sept.	Oct.	Nov.	Dec.	Sept.	Oct.	Nov.	Dec.	Sept.	Oct.	Nov.
Dinoflagellates in thousands .	9	1	0	–	–	0	0	0	–	1	0
Calanus	56	16	3	–	–	0	0	5	–	20	0
Copepods other than Calanus	3008	796	19	–	–	223	69	60	–	218	0
Limacina	0	9	0	–	–	0	0	0	–	35	0
Number of samples . .	1	24	35	–	–	5	14	2	–	2	1

Humber and East Anglian Areas.

The number of samples obtained in these areas is in most of the months very small, too small for more than the briefest notes to be made. The results are tabulated in Table XI. The progressive impoverishment of the plankton as the season advances is seen in each area and in each year.

THE PLANKTON COMMUNITY AS A WHOLE AND THE FEEDING OF THE HERRING.

Hardy (1924) and Savage (1931) in their work on the food of the herring have indicated broadly the succession of food types taken. Hardy found that in the herring, after feeding intensively upon Ammodytes in the early Spring, the diet becomes almost entirely planktonic and in particular, crustacean.

Oikopleura was eaten in May, June and July but mainly in May. The Cladocera, whilst very unimportant compared with forms such as Oikopleura and Calanus, did figure in the food lists and were most numerous in mid-June. Copepods supplied food from March to December, but mainly in June, July and August, particularly in July. We do not know whether Limacina was very abundant in the plankton of that year or not ; it only supplied a relatively small proportion of the food, and that mainly in July and August. Sagitta was fairly important increasing to a maximum in July and August. Savage (1931) found a period of intensive feeding upon Calanus in May, 1926, whilst Temora seemed to be taken mainly in early July with a small peak in early September. Centropages was important in late August and September (particularly off the Yorkshire coast). Paracalanus and Pseudocalanus had maxima in June, but were much more abundant in the food of the Yorkshire coast herring in the period September and October. Savage's findings for the other species are mainly in agreement with those of Hardy. The maxima are Oikopleura in June, Cladocera in June (mainly) followed by a peak composed of Podon in July and a small secondary maximum of Evadne in September and October. Sagitta was most abundant in August and Limacina, which was very abundant in the plankton, increased rapidly in the food in September reaching a maximum in October off the Yorkshire coast.

These findings in general agree very well with the sequence of planktonic forms as found by the Indicator at 7–10 metres' depth. From unpublished information supplied to us by Mr. Savage, we may say that there is a very close agreement between the sequence of different food species in 1932 and the actual sequence in the plankton as shown by the Indicator results. On page 219 we have already commented upon the close agreement found for Calanus in the three years 1931–33 (see Fig. 20), and on page 231 we have demonstrated (1) the marked similarity in the increase of Limacina in the plankton and that in the herring stomachs for 1931 and (2) the marked scarcity of Limacina in the stomachs in 1932 when that form was much less abundant in the plankton samples than in 1931 (see Fig. 23). Both Savage and Hardy are agreed in showing how the feeding decreases with the passage of time, and with the movement of the fishery further south. Whatever this may be due to, there is little doubt that, considering the scarcity of the plankton at this time in the Southern Bight compared with the vast shoals of herring gathered there, very little feeding would be possible however much the herring might desire planktonic food.

SUMMARY.

1. The 704 samples of plankton, taken with the Plankton Indicator by drifters fishing in the Shields, Humber and East Anglian fisheries in the years 1931–33, together with a few off East Anglia in 1930, have been examined and correlated with the associated catches of herring. In addition a series of half-monthly charts has been prepared showing the spatial relations of the waters richer in *Calanus finmarchicus* and the higher herring catches (pp. 183–204).

2. Out of 20 half-monthly periods in the Shields fishery (May to August), 15 show a positive correlation between the abundance of the herring and its food Calanus, and 5 show a negative correlation. The negative correlations tended to occur in July and early August and it is thought that they may possibly be associated with shoals of fish about to spawn (pp. 187 and 222).

3. Poor catches may be made in rich Calanus waters and good catches in poor Calanus waters, but more usually the better catches are made in the richer Calanus waters. There is some evidence that the positive correlations depend most on the general presence of the *highest* catches in the waters *richest* in Calanus (pp. 207–215).

4. An attempt is made to estimate the commercial value of the Indicator if used to locate the richer Calanus waters. The theoretical gain or loss which drifters would be expected to have incurred had they fished only in the richer Calanus waters, is estimated for each period. This is expressed as a percentage gain or loss over the actual catch made when fishing at random. The average of the percentage gains and losses for 1931–33 gives an average gain of 12·7 ± 6·7%, or omitting the incompletely sampled year 1931, the average gain is 21·2 ± 7·5% (pp. 204–209).

5. The histories of individual drifters using the Indicator are followed through the fisheries and the theoretical results of fishing in the richer waters are calculated for each drifter; they all show that substantial gains (averaging 19·3 ± 5·1% over the three years) are to be expected by always avoiding the poorer Calanus water (pp. 215–216).

6. Up to a point it is demonstrated that the richer the Calanus water found the greater may be the expected gain (p. 214).

7. Results off the Humber in September suggest a positive Calanus correlation, but in the East Anglian fishery no satisfactory correlations can be made owing to the scarcity of Calanus and to the fact that the herring are no longer feeding in the late Autumn (p. 202).

8. Observations are made upon the possible grazing effects of the herring upon the stocks of Calanus in the area (pp. 223–224).

9. There are indications that the herring may avoid waters containing large numbers of Limacina, but no definite conclusions have been reached (pp. 226–231).

10. Changes in the fisheries and the plankton are tentatively linked with hydrological changes over the period of the investigations (pp. 224–226).

11. The feeding of the herring in relation to the plankton is considered and notes on the general plankton ecology are included (pp. 232–239).

POSTSCRIPT.

Thirty-six Indicator samples were taken in 1935 by the Boat "A" mentioned above, whilst using the Indicator to locate shoals of fish. Correlations between Calanus and the herring have been made as before and the following data obtained :

Period.	Samples.	Average catch (crans). Lower Calanus.	Higher Calanus.	% Gain or Loss.	Av. Cal.	Av. Limacina.
12th–31st May	10	5·5	3·6	—20·4	11	0
1st–15th June	10	3·2	3·9	+ 9·2	375	3
16th June–1st July	10	2·7	29·8	+83·4	2,455	10
7th–14th July	6	9·6	14·8	+21·3	672	67
Totals	36	21·0	52·1	..	..	..
Averages	..	5·2	13·0	+23·4	..	..

An average gain of 23·4% was made. Limacina was scarce during the whole of this period, though increasing in July, whilst Calanus would appear to have had its maximum in late June.

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Part III. The Zooplankton-Herring Correlations in the Scottish Fisheries.

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With 7 Figures in the Text.

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INTRODUCTION.

THIS section deals with the Plankton Indicator experiments in the herring fisheries in Scottish waters carried out from 1930 to 1933, together with a note on a few results from Irish waters in the spring of 1931. The Scottish waters are here defined as those lying north of latitude 56° N. This extensive area is divided into two sections, the Eastern Fishery and the Western Fishery, by the meridian of 5° W. longitude. The eastern section, being the more important and having been more thoroughly sampled, will be dealt with first.

THE EASTERN FISHERY.

AREA.

The most northerly sample was taken in Lat. 60° 56′ N., and the most easterly in Long. 1° 30′ E.,* so that the area investigated is some 50,000

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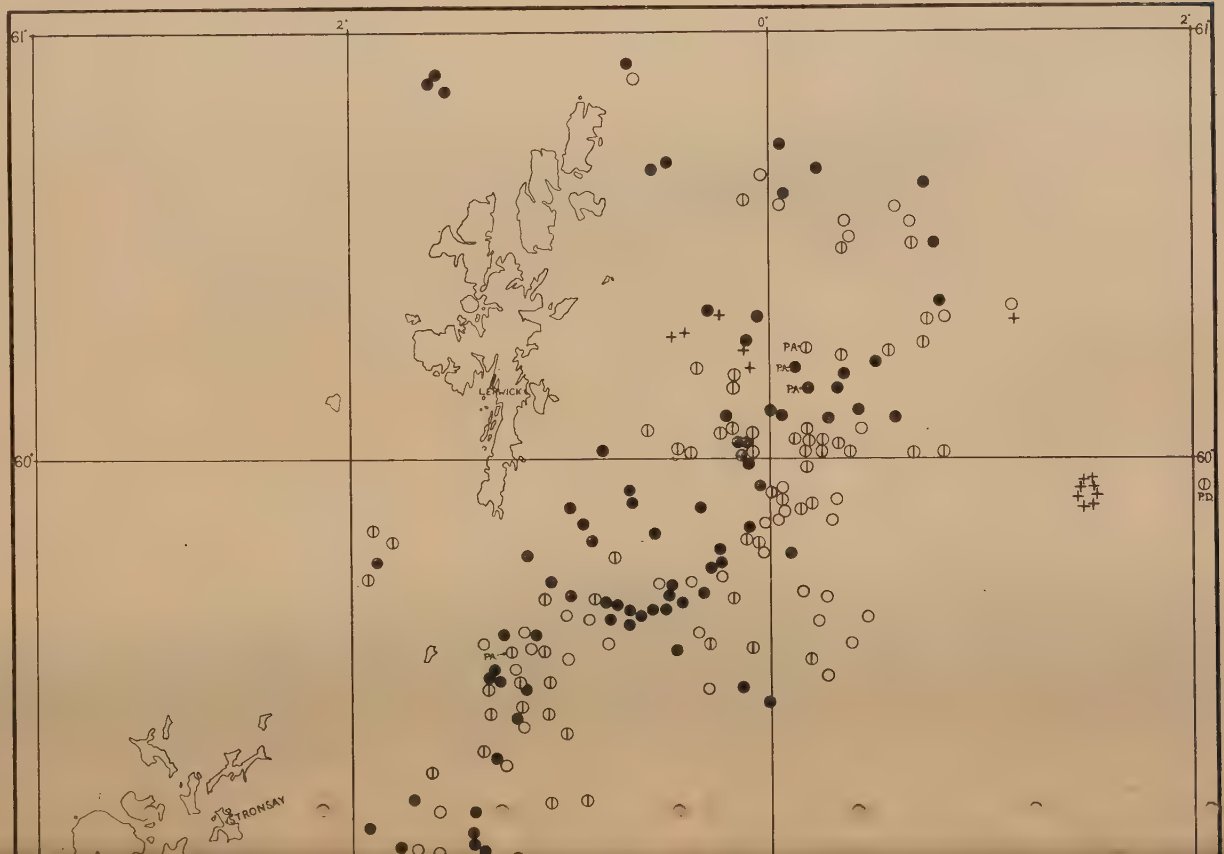
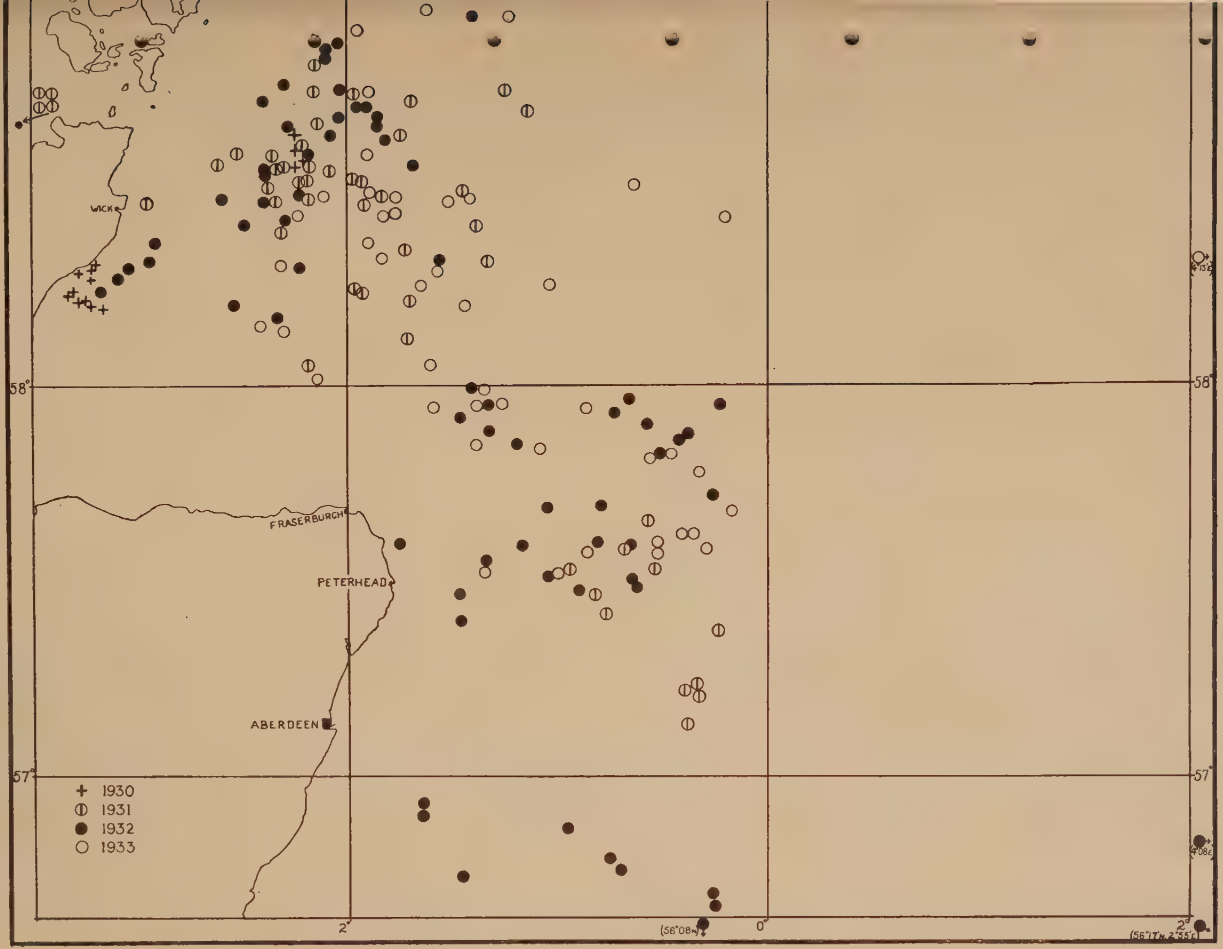
* Excluding three isolated samples in longitudes 2° 55′ E., 4° 08′ E. and 4° 13′ E.

FIG. 1.—Chart showing the distribution of Plankton Indicator samples in the Scottish Eastern Fishery, 1930–1933. (P.D., Position doubtful; P.A., Position approximate. The star indicates that the four samples concerned are situated farther west along the north coast than the chart extends.)


61°
2°
0°
2°
61°
60°
60°
LERWICK
PA
PA
PA
PA
P.D.
STRONSAY


WICK
FRASERBURGH
PETERHEAD
ABERDEEN
58°
58°
57°
57°
2°
0°
2°
(4°13'E)
(4°08'E)
(56°08'N)
(56°17'N. 2°55'E)
+ 1930
⦶ 1931
● 1932
○ 1933

square miles in extent. Ninety per cent of the samples, however, lie within a smaller region of some 18,000 square miles. Even so, in view of the space and time considerations discussed in Part I (p. 161), this is too extensive to be treated as a whole and is divided, by the parallels of latitude of 60° N., 59° N., and 58° N., into four smaller areas (Part I, Fig. 5), which correspond in general to the grounds fished from Lerwick, Stronsay, Wick and Peterhead (and their adjacent ports) respectively. Fig. 1 shows the distribution of the samples taken in the Eastern Fishery.

MATERIAL.

In all, 377 plankton samples were obtained with records of 410 catches of herring, distributed through four summer seasons as follows :—

1930	28	samples	with	46	catches	of herring.
1931	112	,,	,,	117	,,	,,
1932	150	,,	,,	157	,,	,,
1933	87	,,	,,	90	,,	,,

In 1930 all the samples returned were taken by patrol ships,* and were so distributed that several somewhat restricted regions were sampled on occasions separated by considerable intervals of time. In 1931, 1932, and 1933, however, drifters engaged in the fishery took the majority of the samples,† so that the distribution, both in space and time, is much more even. While the 1930 material is insufficient in itself to provide reliable results, we may use it to support those obtained from the more extensive material of the other three years.

ABUNDANCE AND DISTRIBUTION OF CALANUS.

The importance of the copepod *Calanus finmarchicus*‡ in the ecology of the herring is well known (Hardy 1924, Jespersen 1928, Savage 1931), and, since the main correlations are with this species, its abundance and distribution are discussed first.

Table I shows the average numbers of Calanus per sample for half-month periods, the index figures showing the numbers of samples averaged. The two more southerly areas are combined as there are relatively few samples from S. of 57° N. lat., and the Shields figures* are entered for comparison. Omitting the restricted material for 1930 the outstanding features may be summarised as follows :—

---

* Cruisers of the Scottish Fishery Board and gunboats of the Fishery Protection and Minesweeping Flotilla. These have sometimes towed the instrument between the nets of two or more drifters fishing close together (within a distance of a mile) and noted all the catches. This accounts for the number of catches being greater than the number of samples.

† The methods of using the Indicator from patrol ships and drifters are described in Part I, page 153.

‡ Where the term Calanus is used in this paper the species *Calanus finmarchicus* (Günn.) is referred to.

(1) There appears to be a progressive increase in the abundance of Calanus over the three years, the average numbers being 125 for 1931, 241 for 1932 and 894 for 1933 (these figures being based on 112, 150 and 87 samples respectively). Restricting the material to that obtained between mid-June and the end of July, a period well sampled in all the years, the figures are a little lower but show the same upward trend as follows :—111 for 1931, 197 for 1932 and 724 for 1933 (based on 97, 109 and 69 samples respectively). These figures confirm the conclusion of Ogilvie (1934) who, comparing 1933 with 1931, says Calanus "was considerably more abundant in 1933." It is worthy of note here that the influx of Atlantic water into the North Sea was greater than usual in 1932 and 1933, particularly in the latter year.†

TABLE I.

Average Calanus per Sample per Half-month.

Year.	Area.	May 16–31	June 1–15	June 16–30	July 1–15	July 16–31	August 1–15	August 16–31
1930	N. of 60° N.		175^{5}	—	—	0^{1}		
,,	59°–60° N.			897^{8}				
,,	S. of 59° N.					8^{4}	16^{10}	
1931	N. of 60° N.			326^{15}	49^{8}	93^{5}		
,,	59° to 60° N.		11^{2}	110^{9}	82^{10}	161^{11}		
,,	S. of 59° N.			35^{8}	5^{11}	63^{17}	272^{11}	
,,	Shields		41^{6}	99^{24}	64^{21}	76^{37}	93^{17}	68^{29}
1932	N. of 60° N.			188^{10}	7^{13}	127^{8}		
,,	59° to 60° N.			102^{18}	57^{9}	145^{21}	1420^{1}	
,,	S. of 59° N.	512^{3}	1375^{1}	—	279^{16}	620^{14}	306^{28}	265^{6}
,,	Shields	474^{43}	864^{50}	912^{45}	189^{32}	—	175^{11}	99^{21}
1933	N. of 60° N.			458^{7}	817^{3}			
,,	59° to 60°		2947^{9}	1330^{17}	688^{5}			
,,	S. of 59° N.		283^{3}	448^{11}	389^{15}	682^{11}	93^{5}	
,,	Shields		200^{40}	389^{38}	1022^{25}	648^{25}	70^{39}	

---

* For further information relating to the abundance of Calanus in the Shields Fishery, see Part II.

† Strong Atlantic inflow resulted in temperatures $1\frac{1}{2}$° to 2° C. greater than normal in 1932, 2° to 3° C. in 1933, and salinities described as "higher than usual" in the summer of 1932, and "unusually high" in surface layers in the extreme north, and in sub-surface layers farther south, in June and July of 1933. Further evidence is the recovery of drift bottles liberated in Scottish waters from the coasts of Lincolnshire, Norfolk and Suffolk, a somewhat unusual occurrence. Also significant numbers of such drift bottles were recovered from the Danish coast south of 56° 30′ N. Lat. (Ann. Rep. Fish. Bd. Scot. 1933 and 1934.) See also Part II (p. 224).

(2) In each of the three years there is a general tendency for the Calanus numbers to be low in the first half of July.* Gibbons (1933) finds for earlier years that June and September are the periods of greatest abundance in the area South of 58° 45′ N., but that North of this July is the month of maximum numbers. Differences in the vertical distribution of Calanus in the northern and southern parts of the area in the summer months may explain the difference between our results in the area N. of 59° N. and those of Gibbons, since our sampling is confined to a depth of 7–10 metres (the region of the herring nets) while Gibbons' material is largely from vertical hauls. However, it should be noted that Lucas shows, for the Shields area (Part II, p. 219), how in general the variations in the Calanus numbers taken by the Indicator (at 7–10 metres) correspond with the fluctuations in the numbers found by Savage in the herring stomachs during the same period. The figures showing the abundance of Calanus for the area South of 59° N., while not extensive enought to permit a detailed comparison, indicate a general agreement with Gibbons' results.

CALANUS-HERRING CORRELATIONS.

Since there are such wide differences in the ranges of Calanus numbers in different areas and at different seasons it is not possible to adopt a fixed scale with which to correlate the herring catches. The method adopted is discussed in detail by Prof. Hardy in Part I (pp. 161–164), and briefly is as follows :—The samples in each area are grouped into short-time periods, and for each area-period the samples, with their corresponding catches, are arranged in ascending order of Calanus numbers : the series thus formed is divided into two parts, one containing the lower half, and the other the higher half, of the Calanus numbers. The catches corresponding to the samples in each half can then be compared. Examples of two such correlations are given on pages 162 and 163 of Part I.

In the Scottish Fisheries the half-month† was adopted as the shortest time-period which gave a reasonable number of "units" (i.e. Calanus sample and corresponding herring catch) in the correlation, and we have fixed 10 as the number of units required to form a "valid" or "primary" table from which deductions may be made. Tables for those area-periods which have only 6 to 9 units have been drawn up, but will be termed "secondary," and will only be used to indicate the probable trend of the correlations. These are listed separately from the primary tables. Periods having less than 6 units available have been discarded.

---

* The writer, working in a drifter to the eastward of the Shetlands during the middle of July, 1932, found very few Calanus in the samples obtained (rarely more than *ca.* 25) although a fairly wide area was covered, and samples taken frequently when steaming in addition to those taken just before shooting.

† Occasionally, at the beginning or end of a period, an odd day, not otherwise included, has been added to increase the number of units in a correlation, e.g. 16 July to 1 August, 1932.

There are twenty primary area-periods during the four years 1930 to 1933 and eleven secondary area-periods ; Tables II and III below show their distribution and indicate the sign of the correlation in each, i.e. whether it is positive in that more herring were taken in the richer Calanus water, or negative in that fewer herring were taken in such water.

TABLE II.

Primary Correlation Tables.

Area.	1930.	1931.	1932.	1933.
N. of 60° N.		16–30 June +	16–30 June +	
			1–15 July +	
59° to 60° N.	16–30 June +	1–15 July +	16–30 June +	16–30 June –
		16–31 July +	16 July–1 Aug. +	
58° to 59° N.	1–15 Aug. –	16–30 June +	1–15 Aug. –	1–15 July +
		1–15 July +		16–31 July +
		16–31 July +		
56° to 58° N.		31 July–15 Aug. +	1–15 July –	16–30 June –
			1–15 Aug. +	

TABLE III.

Secondary Correlation Tables.

Area.	1930.	1931.	1932.	1933.
N. of 60° N.	1–15 June +	1–15 July +	16–31 July +	15–30 June –
59° to 60° N.		16–30 June +	1–15 July –	1–15 June +
				1–15 July +
58° to 59° N.	16–31 July +		16–31 July +	
56° to 58° N.			16–31 July –	

Table II above shows fifteen positive and five negative correlations, and in Table III the eleven secondary area-periods suggest eight positive and three negative correlations. We see that on the whole the tendency of the correlations is positive. The secondary tables support in detail, as well as in general, the main results. Summaries of the results of these correlations of primary and secondary periods are shown in Tables IV and V respectively.

It is interesting to note how closely the results for the Shields Fishery (Part II, p. 209) agree with those for the Scottish Fishery. For the Shields Fishery the "all boat" results give fifteen positive and five negative correlations, and the "individual boat" results twenty-three positive and eight negative correlations. That is, in each series, two Scottish and two Shields, we find a three-to-one ratio of positive to negative correlations.

COMMERCIAL SIGNIFICANCE OF THE CALANUS-HERRING CORRELATIONS.

A brief statement of the results of the correlation tables, as such, has been given above, and the next step is to show how these results are of value to the herring fishery if the Indicator is used as a means of locating the water rich in Calanus. The commercial application of the Indicator is discussed in Part I (p. 165). The results of the correlations, expressed as being positive or negative, are not sufficient to enable an evaluation of the method to be attempted, so that a " term " must be found which is common to all the correlations and independent of variations in range of Calanus figures and catches. The method of obtaining such a " term," in the form of the gain or loss which would have resulted from avoiding the waters poorer in Calanus, expressed as a percentage of the total actual catch, is demonstrated, with examples, in Part I (p. 162), and Table IV gives these figures (in col. 13) for all the primary correlations, Table V giving the secondary results. The reasons for adopting this method of evaluating the correlations rather than one of a number of other methods are fully discussed in Parts I (p. 161) and II (p. 180).

The correlation tables for 1930, for two primary and two secondary area-periods, differ from those for the other years in that each is based on material collected by a patrol ship on a single day within a very restricted area.* In one table, for 7th August, where a markedly negative correlation is found, sixteen of the nineteen samples had Calanus numbers ranging from 0 to 20 and the highest did not exceed 100. These 1930 results are not, therefore, included with those of the other three years except where stated.

For the years 1931 to 1933 there are eighteen primary area-period correlation tables. Five of these tables show a gain or loss not greater than 10%, which might commercially be regarded as unimportant† and so will be termed " neutral." Of the remaining thirteen, eleven show gains ranging from 12·3% to 85·2% and two show losses of 11·1% and 30·4%. The eighteen tables show an average gain of 24·5%.

Nine secondary area-period tables during 1931–33 indicate results as follows :—four are neutral, four indicate gains ranging from 28·5% to 100%,‡ and one indicates a loss of 100%.§ These secondary tables when combined indicate an average gain of 16·4%.

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* The most extensive group only covered an area about 8 × 5 miles.

† These results average a gain of 0·5%.

‡ All catches in poorer Calanus water blank, total catch in richer Calanus water 7·5 crans.

§ All catches blank, except one of 5·75 crans in poorer Calanus water.

TABLE IV.

SUMMARY OF DATA RELATING TO THE CALANUS-HERRING CORRELATIONS IN THE SCOTTISH FISHERIES 1930 TO 1933, FOR PRIMARY PERIODS ONLY.

Year.	Period.	Area.	No. of Samples.	Calanus Range.	Calanus Av.	Catch (in crans). Range.	Catch (in crans). Av.	Total catch in water of Lower Calanus Numbers.	Total catch in water of Higher Calanus Numbers.	Average catch in water of Lower Calanus Numbers.	Average catch in water of Higher Calanus Numbers.	Percentage Gain or Loss on total catch.
1930	16–30 June	59° to 60° N.	10	510–1360	922	23·00–55·75	43·00	188·75	241·00	37·8	48·2	+12·2
	1–15 Aug.	58° to 59° N.	19	0–100	21	0·00–30·00	5·40	96·50	6·50	10·2	0·7	−87·4
1931	16–30 June	N. of 60° N.	15	0–1560	326	0·00–50·00	12·60	82·75	106·00	11·0	14·1	+12·3
	,,	58° to 59° N.	13	4–74	40	0·00–5·50	1·00	3·75	9·00	0·6	1·4	+41·2
	1–15 July	59° to 60° N.	10	0–416	82	0·00–6·00	2·00	9·00	10·50	1·8	2·1	+ 7·7
	,,	58° to 59° N.	11	0–40	5	0·00–38·00	7·70	20·75	64·25	3·8	11·7	+51·2
	16–31 July	59° to 60° N.	11	1–800	161	0·00–27·00	8·20	17·50	72·50	3·2	13·2	+61·0
	,,	58° to 59° N.	15	0–200	64	0·00–5·50	1·20	4·30	14·10	0·6	1·9	+53·1
	31 July–15 Aug.	56° to 58° N.	11	14–656	261	0·00–3·50	1·20	1·00	12·50	0·2	2·3	+85·2
1932	16–30 June	N. of 60° N.	10	0–515	188	4·00 35·00	15·00	72·50	77·50	14·5	15·5	+ 3·3
	,,	59° to 60° N.	19	0 395	97	0·00–90·00	22·80	183·125	250·725	19·3	26·4	+15·6
	1–15 July	N. of 60° N.	13	0–50	5	0·00–40·00	10·10	62·92	68·59	9·7	10·6	+ 4·3
	,,	56° to 58° N.	12	0–865	222	1·00–14·00	8·30	54·50	45·50	9·1	7·6	— 9·0
	16 July–1 Aug.	59° to 60° N.	22	1–1420	194	0·00–72·00	22·80	157·00	345·25	14·3	31·4	+37·5
	1–15 Aug.	58° to 59° N.	22	0 820	184	0·00–30·00	5·10	73·50	39·25	6·7	3·6	—30·4
	,,	56° to 58° N.	10	5–1080	510	0·00–17·00	5·30	21·50	31·25	4·3	6·25	+18·5
1933	16–30 June	59° to 60° N.	19	88 4200	1306	0·00–52·00	14·40	142·40	131·90	15·0	13·9	— 4·0
	,,	56° to 58° N.	10	10–2000	393	1·00–30·00	12·15	67·50	54·00	13·5	10·8	—11·1
	1–15 July	58° to 59° N.	11	0–1580	423	0·00–71·00	13·30	58·00	88·25	10·6	16·1	+20·7
	16–31 July	58° to 59° N.	11	0–1415	682	0·00–30·00	3·90	3·50	39·50	0·6	7·2	+83·7

TABLE V.

SUMMARY OF DATA RELATING TO THE CALANUS-HERRING CORRELATIONS IN THE SCOTTISH FISHERIES 1930 TO 1933, FOR SECONDARY PERIODS ONLY.

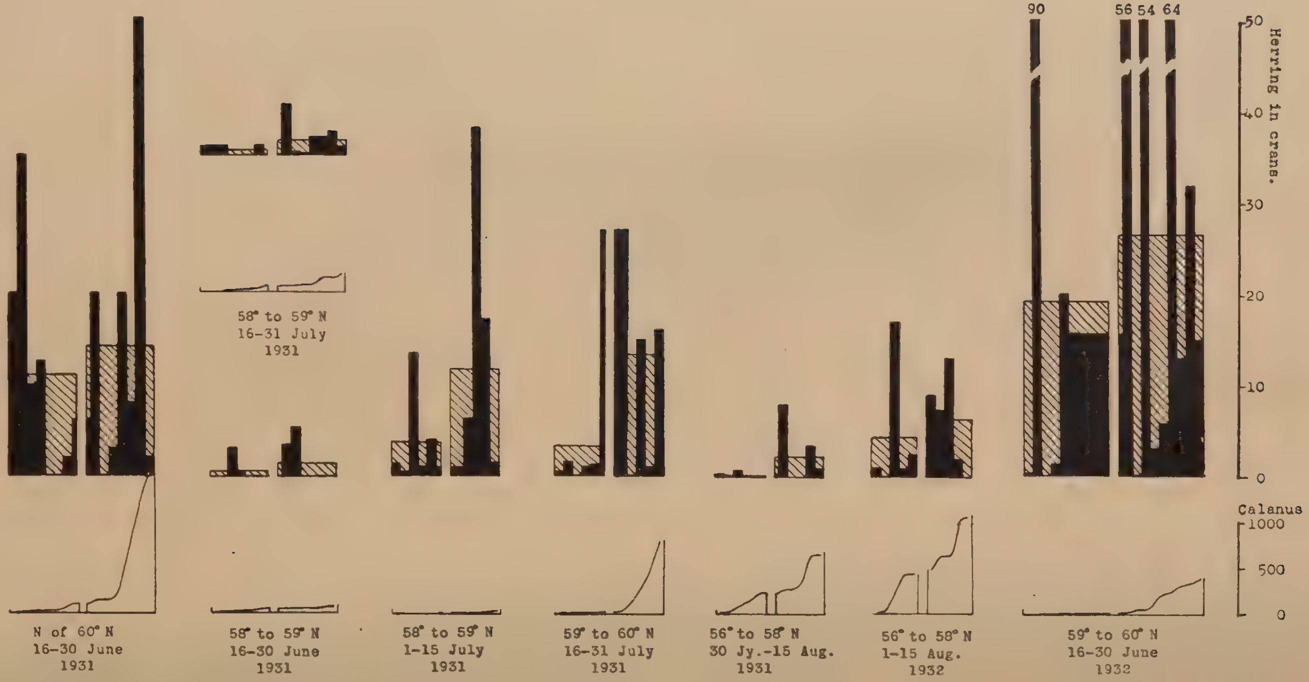
Year.	Period.	Area.	No. of Samples.	Calanus		Catch (in crans).		Total catch in water of		Average catch in water of		Per-centage Gain or Loss on total catch.
				Range.	Av.	Range.	Av.	Lower Calanus Numbers.	Higher Calanus Numbers.	Lower Calanus Numbers.	Higher Calanus Numbers.	
1930	1–15 June	N. of 60° N.	7	64–300	191	6·50–69·00	29·10	80·70	123·30	23·1	35·2	+20·9
	16–31 July	58° to 59° N.	9	0–16	8	1·00–3·00	1·75	6·40	9·40	1·4	2·1	+19·0
1931	16–30 June	59° to 60° N.	9	1–450	110	3·00–40·00	20·60	92·00	93·50	20·4	20·8	+ 0·8
	1–15 July	N. of 60° N.	8	3–160	49	0·00–100·00	15·30	13·75	109·00	3·4	27·3	+77·6
1932	1–15 July	59° to 60° N.	9	1–244	57	0·50–25·00	6·90	32·00	30·25	7·1	6·7	— 2·8
	16–31 July	N. of 60° N.	8	0–540	127	1·00–61·25	12·20	27·30	70·20	6·8	17·5	+43·9
	,,	58° to 59° N.	8	132–1075	331	1·00–35·25	18·20	71·75	74·00	17·9	18·5	+ 1·5
	,,	56° to 58° N.	6	60–3155	1005	1·00–25·00	10·70	32·75	31·50	10·9	10·5	— 1·9
1933	1–15 June	59° to 60° N.	9	22–8000	2947	0·00–53·00	18·50	59·50	107·00	13·2	23·8	+28·5
	15–30 June	N. of 60° N.	7	32–1400	458	0·00–5·75	0·80	5·75	0·00	1·6	0·0	—100·0
	1–15 July	59° to 60° N.	6	80–1640	587	0·00–5·00	1·25	0·00	7·50	0·0	2·5	+100·0

The details of these gains and losses are shown in tabular form, primary results being shown in heavy type, as follows :—

Gains		Neutral.		Losses.	
85·2%	100·0%	**7·7%**	1·5%	– **11·1%**	– 100·0%
83·7%	77·6%	**4·3%**	0·8%	– **30·4%**	
61·0%	43·9%	**3·3%**	– 1·9%		
53·1%	28·5%	– **4·0%**	– 2·8%		
51·2%		– **9·0%**			
41·2%					
37·5%					
20·7%					
18·5%					
15·6%					
12·3%					

It is important that the values for the individual periods should not be stressed, as the results for any individual period may be affected by the fortuitous nature of the fishing. The value of these results lies in their consideration as a whole, and Prof. R. A. Fisher suggested that the significance of the different series of tables should be demonstrated by the estimation of their Standard Errors. Thus the primary correlations for the years 1931–33 give an average gain of 24·5 ± 7·7% (‘ t ’ 3·182), while if the year 1930 is included the result becomes 18·3 ± 8·9% (‘ t ’ 2·056). The secondary correlations, as should perhaps be expected, do not approach this level of reliability, 1931–33 giving an average gain of 16·4 ± 19·1% (‘ t ’ 0·859) and 1930–33 17·0 ± 15·5% (‘ t ’ 1·097). Fig. 2 shows graphically the details of the catches in the poorer and richer Calanus waters for each of the periods of gain, and Fig. 3 for each of the periods of loss. The neutral periods are not figured. The average catches in poorer and richer Calanus waters are also shown, superimposed on the individual catches. These figures show quite clearly that the position in the Calanus range of one high catch in a period may weight the result, in that it may dominate the other figures wherever it falls. The higher catches do not all occur in the richer Calanus waters, an appreciable number falling in the poorer waters, but it is found that more high catches occur in the richer Calanus waters than in the poorer. Conversely more blank catches occur in the poorer Calanus waters than in the richer. Catches of intermediate value are more equally distributed. The following table shows the numbers of occurrences of catches of different magnitudes in the poorer and richer Calanus waters.

Herring catches, Range.	Numbers of Occurrences in Poorer Calanus waters.	Richer Calanus waters.
0·0 crans	33	27
0·1–5·0 ,,	52	49
5·1–10·0 ,,	27	25
10·1–20·0 ,,	22	18
20·1–30·0 ,,	9	9
Over 30·0 ,,	7	22



Herring in crans.
50
40
30
20
10
0
Calanus
1000
500
0
90
56
54
64
N of 60° N
16-30 June
1931
58° to 59° N
16-31 July
1931
58° to 59° N
16-30 June
1931
58° to 59° N
1-15 July
1931
59° to 60° N
16-31 July
1931
56° to 58° N
30 Jy.-15 Aug.
1931
56° to 58° N
1-15 Aug.
1932
59° to 60° N
16-30 June
1932

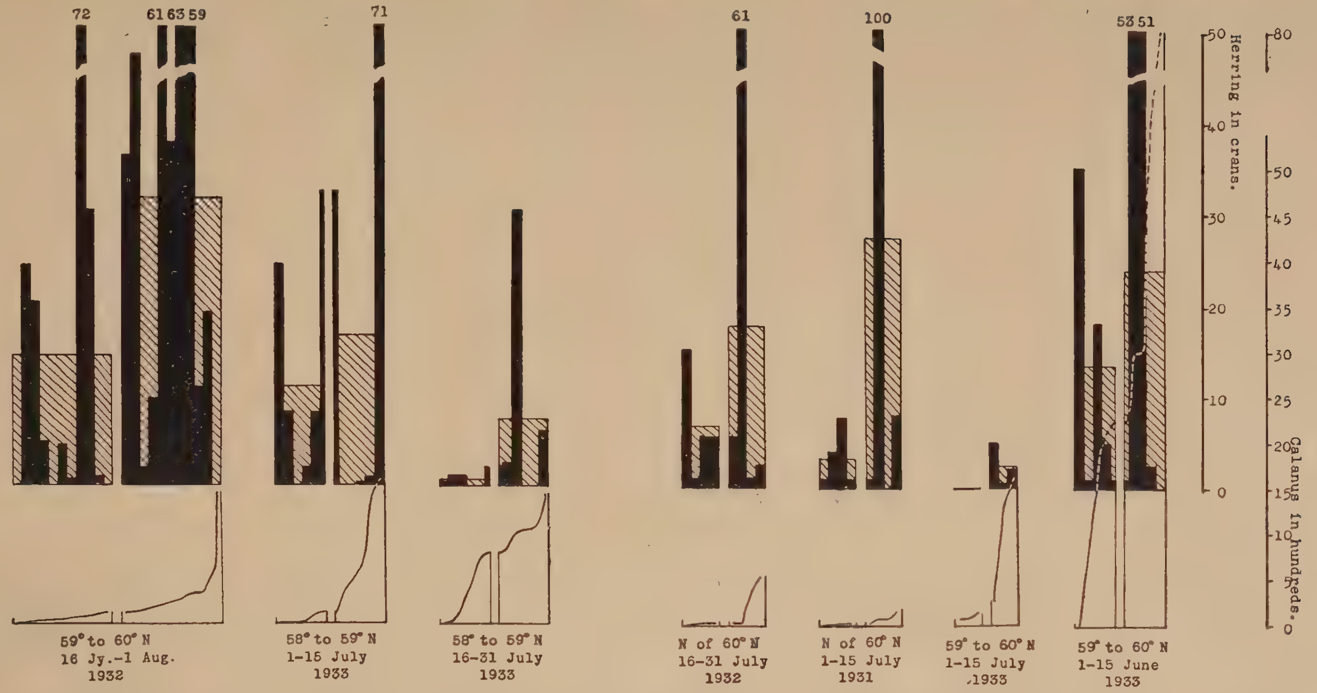


FIG. 2.—Histograms showing (in black) the individual catches of herring in each area-period which showed a theoretical *gain* of over 10% (see text). There are fifteen such area-periods, eleven of which are primary (with 10 or more catches) and are shown first, and four secondary (6–9 catches) shown last. In each period the catches are arranged from left to right in the order of ascending values of Calanus in the associated plankton samples; each series is divided into halves, the left half representing the catches in the poorer and the right half those in the richer Calanus water. The average catches of herring in each half are shown as shaded histograms. Below each histogram is a graph showing the associated Calanus values. The diagrams are in fact graphical representations of the area-period tables drawn up for correlation purposes.

Fig. 4 shows the percentage of catches below given values which occur in the poorer and richer Calanus waters, the years 1931, 1932 and 1933 are shown separately, and the combined result is also given. It is seen that in the poorer Calanus waters the percentage of catches below any given level is greater than that in the richer Calanus waters, and that in the combined curve for 1931–33 the difference tends to increase when the higher catch levels are reached.

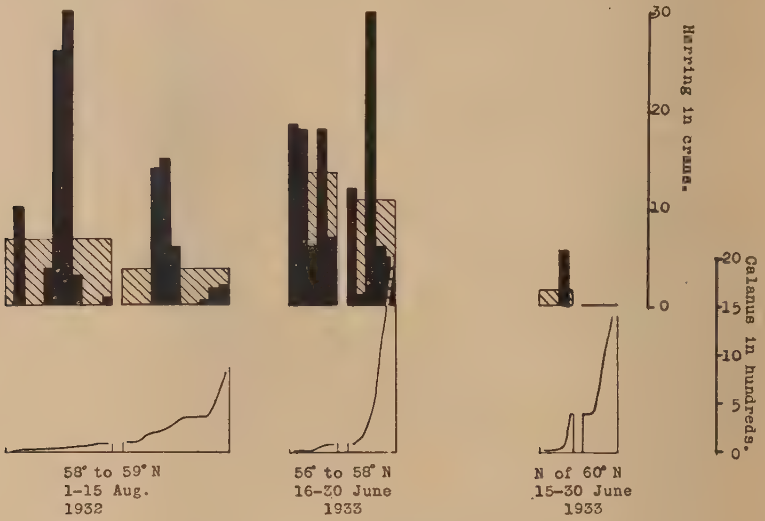


Fig. 3.—Diagrams of the same kind as those in Fig. 2, but for those area-periods showing a theoretical *loss* of over 10% (see text). Two of these are primary area-periods (10 or more catches) and one is a secondary area-period (7 catches).

There is a noticeable difference in the distribution of catches of various magnitudes in the Shields Fishery (Part II, p. 211) and the Scottish Fishery. Whereas in the latter for the years 1931–33 20·0% of the total catches are blank and 15·7% are over 20 crans, in the Shields Fishery for the years 1932–33 only 9·4% are blank and only 5·3% exceed 20 crans.* That is, more high catches were secured in the Scottish Fishery, but there was a greater chance of getting a blank haul; in the Shields Fishery

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* Percentage occurrences of blank catches and catches over 20 crans are as follows for individual years. The 1931 Shields figures are not used here (see Part II, p. 210).

	Scotland.				Shields.		
	No. of samples.	% blank.	% over 20 crans.		No. of samples.	% blank.	% over 20 crans.
1931	103	28·2	10·7				
1932	139	16·5	20·1	1932	214	9·8	1·0
1933	73	27·4	19·2	1933	190	8·9	10·0

blank hauls were relatively less frequent, but on only a few occasions was a really high catch obtained.

The results outlined above indicate the nature of the benefit which could be derived by the fishermen from consistent use of the Plankton Indicator on the basis of the Calanus-Herring Correlations. Over a long period more higher catches, and fewer blank catches, will be the result of fishing always in waters giving the larger numbers of Calanus, although it would be necessary to use discretion in determining how much extra time may reasonably be spent in looking for such waters.

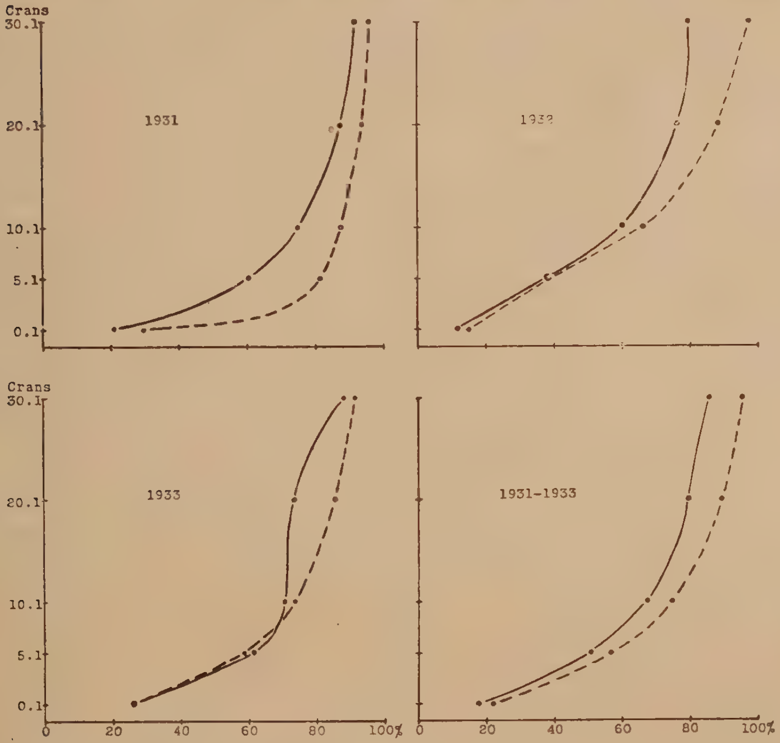

FIG. 4.—The broken-line curves show for the catches taken in the poorer Calanus water the percentage falling below given values (vertical scale), and the continuous-line curves show the corresponding percentages for the catches taken in the richer Calanus water. They show that the larger catches are taken more frequently in the richer Calanus water.

Owing to the fortuitous nature of the fishing it would be necessary to continue these investigations over a long period of years, and to have many more samples in each year, before we could discuss with certainty the seasonal variations in the degree of correlation between Calanus and herring, and thus the variations in the efficiency of the Indicator as a commercial instrument. Our results do, however, indicate that an increasing gain may be expected from mid-June to the end of July, and this increase is evident in the individual years as well as in the combined result (Fig. 5).

TABLE VI.

Percentage Gains and Losses in Areas and Periods.

Year.	Area.	June 1–15	June 16–30	July 1–15	July 16–31	August 1–15
1930	N. of 60° N.	+ 20·9^{7}				
1931			**+ 12·3**^{15}	+ 77·6^{8}		
1932			**+ 3·3**^{10}	**+ 4·3**^{13}	+ 43·9^{8}	
1933			− 100·0^{7}			
1930	59° to 60° N.		**+ 12·2**^{10}			
1931			+ 0·8^{9}	**+ 7·7**^{10}	**+ 61·0**^{11}	
1932			**+ 15·6**^{19}	− 2·8^{9}	**+ 37·5**^{22}	
1933		+ 28·5^{9}	**− 4·0**^{19}	+ 100·0^{6}		
1930	58° to 59° N.				+ 19·0^{9}	**− 87·4**^{19}
1931			**+ 41·2**^{13}	**+ 51·2**^{11}	**+ 53·1**^{15}	
1932					+ 1·5^{8}	**− 30·4**^{22}
1933				**+ 20·7**^{11}	**+ 83·7**^{11}	
1931	56° to 58° N.					**+ 85·2**^{11}
1932				**− 9·0**^{12}	− 1·9^{6}	**+ 18·5**^{10}
1933			**− 11·1**^{10}			

Table VI shows the figures for all the results, primary (in heavy type) and secondary, and the average overall gains, for primary periods only, in the different areas are as follows :—

Area			
	N. of 60° N.	+ 6·6%	based on 3 tables.
	59° to 60° N.	+23·6%	,, 5 ,,
	58° to 59° N.	+36·6%	,, 6 ,,
	56° to 58° N.	+20·9%	,, 4 ,,

and in each year there is a resultant net gain for all area-periods.

1931.	1932.	1933.	1931–33.
+44·5%	+5·7%	+22·3%	+24·5%

If the two primary area-periods for 1930 are included the average for 1930–33 is +18·3%, but on page 250 it is shown that there are good grounds for omitting these results from the general conclusions.

Table VI also shows that the general increase in gain from 16–30 June to 16–31 July, indicated by the average curve in Fig. 5, occurs, almost without exception, in each year in each area where sufficient figures are available. Even where the 16–30 June figure is a loss, it is seen

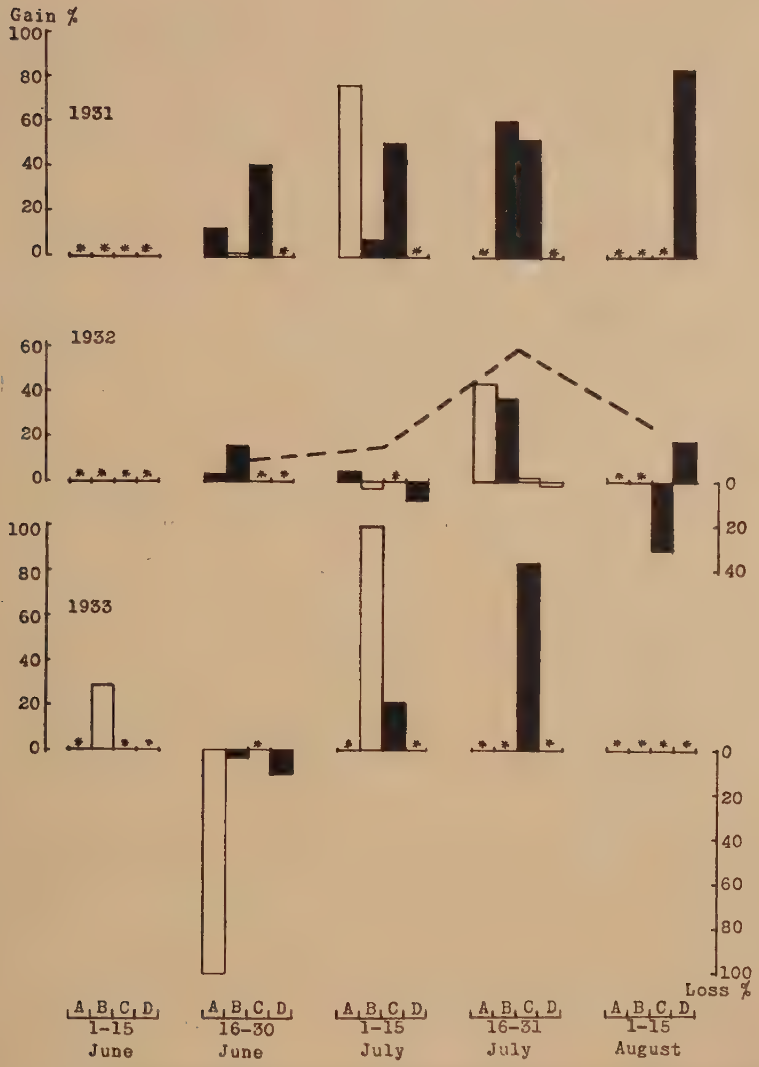

FIG. 5.—Histograms showing the variations in the Calanus-herring correlations, expressed as theoretical percentage gains or losses (see text), for the area-periods in the Scottish Eastern Fishery for the years 1931, 1932 and 1933. The areas N. of 60° N., 59° to 60° N., 58° to 59° N. and 56° to 58° N. are indicated by the letters A, B, C and D respectively. The primary area-periods are shown as black histograms and the secondary area-periods as open histograms. Asterisks indicate that too few samples were obtained to make even a secondary period. The broken-line curve, superimposed on the 1932 base, indicates the trend of the seasonal variation in the primary correlations, obtained by averaging all the primary results available in each period.

that the loss diminishes or turns to a gain in the subsequent periods (excluding 1–15 August). Two secondary results in 1–15 June indicate gains higher than the average for the second half of the month, but this cannot be confirmed on the limited material available.

The course of the Summer Fishery is described by Wood (1930) who states that it " begins in May or early in June and is continued generally till about the middle of September, i.e. from the time that the reproductive organs of the Autumn spawners begin to develop until spawning is completed and the bulk of the spent fish has left the fishing grounds." The seasons over which this work extends have, however, been shorter; full-scale operations have rarely commenced till the second, or even the third, week in June,* so that our material, which is scanty in May and early June, does in fact cover the beginning of the fishery in the years concerned. The end of the fishery is less satisfactorily sampled, as although in the Northern waters (Shetlands and Orkneys) large-scale operations have ceased about the end of July, further south they have continued till the end of August or first week in September, and after mid-August we have little material as the drifters taking samples have rarely finished the season in these waters.

The main period of high productivity (mid-June to mid-July) is, however, fairly well represented, and fair numbers of samples are available for the second half of July. In August material is less plentiful, only four correlation tables, one of which is for 1930, being possible, giving rather erratic results. It is possible that this wide variation in the August results is associated with the fact that, at this time, the shoals fished are composed mainly of spawners and spents, when catches are much more variable than at any other time. According to Wood (ibid. p. 9) a suitable condition of tide and weather, i.e. a considerable amount of sea disturbance, is by far the most important factor in determining the chances of a good catch of ripe herring; heavy catches of spents are not infrequent, but are rarely maintained for long on account of the rapid dispersal of the shoals after spawning. In each of the three years, 1931–33, periods of calm weather occurred in the Scottish Eastern Fishery in August. Spents formed an appreciable proportion of the landings after about the first week of August, and when the calm weather occurred the average catch level dropped to a low value. Any incidence of rough weather gave an increase in average catch.† Under these conditions it is not to be expected that the Indicator results will be absolutely reliable.

Although the number of drifters taking samples is relatively small, the curves expressing the weekly average landings of these boats, while not absolutely coincident with the curves showing the weekly average landings at the ports (Fig. 6), do indicate fairly exactly the changes in productivity through the season and are thus sufficiently representative of the work of the fleet to render the results obtained in this work applicable to the fishery as a whole. We are indebted to the Fishery Board for Scotland for permission to use their figures and for putting at our disposal the data necessary for determining the weekly average landings at the ports.

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* Due to agreements within the trade fixing dates for the commencement of curing.

† Weekly reports on the Herring Fisheries in *The Fishing News* and *The Fish Trades Gazette* are the sources of this information.

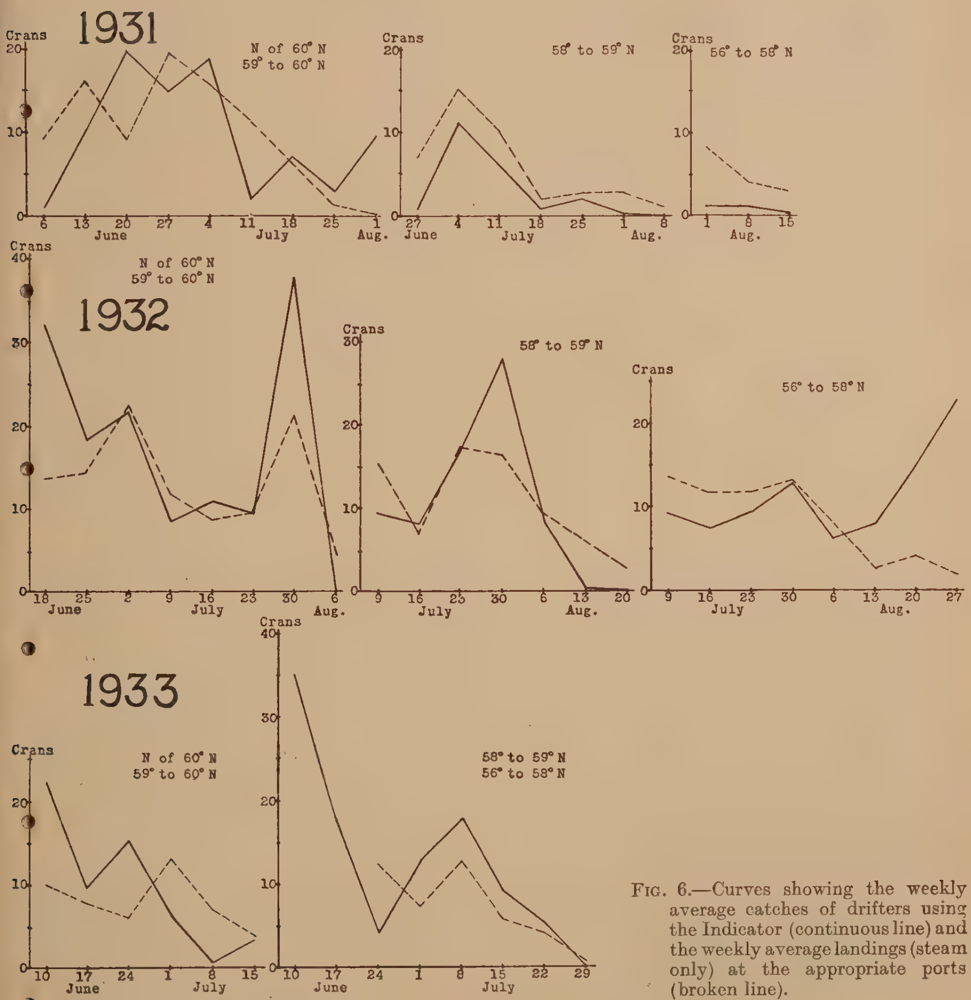

FIG. 6.—Curves showing the weekly average catches of drifters using the Indicator (continuous line) and the weekly average landings (steam only) at the appropriate ports (broken line).

An interesting example of the way in which these results can be applied to the fishery and evaluated may conveniently be quoted here. On the 23rd June, 1932, in the area 59° to 60° N. sufficient units are available to enable a correlation table to be compiled for this one day in the period 16–30 June. The material is all from an area to the south-east of Lerwick, triangular in shape with the apex pointing north-west and about twenty miles from apex to base. The higher Calanus numbers were more to the south-east than the lower (Fig. 7 shows the distribution of Calanus and catches) so that boats steaming only 20 to 25 miles off did not reach the area of richer Calanus, while those going 30 miles or more did get into good Calanus waters.

TABLE VII.

Calanus-Herring Correlation Table.

Area, 59° to 60° N. 23rd June, 1932.

	Lower Calanus numbers.		Higher Calanus numbers.	
	Calanus.	Herring in crans.	Calanus.	Herring in crans.
	1	0·0	395	15·0
	10	0·0	305	13·0
	10	0·0	260	64·0
	10	2·2	60	54·0
	10	50·0	21	56·0
Total	41	52·25	1041	202·0
Average	8^5	$10{\cdot}45^5$	208^5	$40{\cdot}4^5$

Grand total catch : 254·25 crans for 10 landings.

If all the catches had been made in waters of the richer Calanus values the expected (theoretical) total catch would have been 404·0 crans ; i.e. a theoretical gain of 149·75 crans over the actual total catch obtained when fishing at random. This may be expressed as a (theoretical) gain of 58·9%.

The boats going farthest, i.e. getting into good Calanus waters, would have gained 30 crans apiece or *ca.* 300% over the boats which did not steam so far, and 15 crans or 58·9% over the average for all the boats fishing on that ground. The average landing at the port the next morning (24th June) was 18 crans* and prices were 15s. 3d. per cran for curing

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* *Fishing News*, 2nd July, 1932.

(Russian contract) and 25s. per cran for freshing, so that boats which got into the richer Calanus waters would have made 22 crans over the average and have been anything from £16 15s. 6d. to £27 10s. up on the night's fishing.

This example is quoted to show that these results can be evaluated and applied to the fishery, and, although it is realised that during periods of glut the use of the instrument to find the best fishing ground may be of less value, yet even here it may help to reduce the cost of catching the same amount of fish that would be obtained by fishing without its aid.

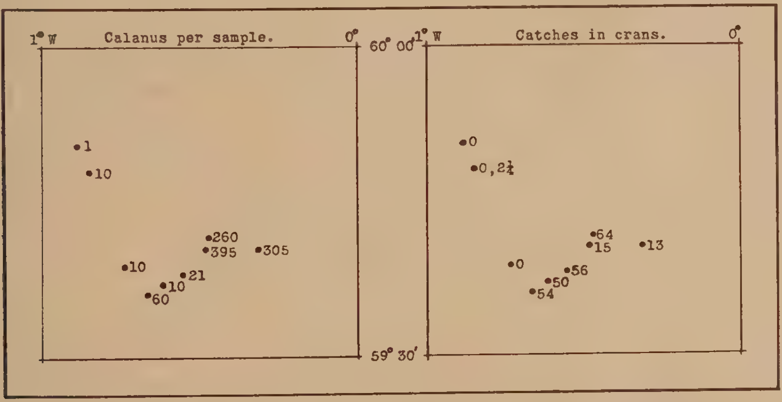

Fig. 7.—Showing the distribution of Calanus from Indicator samples (left-hand chart) and the associated herring catches (right-hand chart) for the 23rd June, 1932.

The reservation (discussed on p. 260) regarding the latter part of the fishery (August) will need to be borne in mind when applying these results commercially.

ABUNDANCE AND DISTRIBUTION OF LIMACINA.

The negative correlation of herring catches with numbers of Limacina* is discussed in Part I (p. 160) and an account of the distribution of this form in the Scottish waters precedes here the detailed discussion of these correlations and their significance.

In the limited material from 1930 Limacina is recorded in only two of the four series of samples (59°–60° N., 17th June, average 15; and S. of 59° N., 7th August, average 1). Table VIII shows the average numbers of Limacina per sample for half-monthly periods for the years 1931 to 1933; the two more southerly areas have been combined as was done for Calanus,

* The term Limacina used throughout this paper refers in general to *Limacina retroversa* (Flemming). See also Part II, page 179, footnote †.

and the Shields figures* are entered for comparison. The index figures show the number of samples averaged.

TABLE VIII.

AVERAGE LIMACINA PER SAMPLE PER HALF-MONTH.

Year.	Area.	May 16–31.	June 1–15.	June 16–30.	July 1–15.	July 16–31.	August 1–15.	August 16–31.
1931	N. of 60° N.			14^{15}	2^{8}	5^{5}		
	59° to 60° N.		4^{2}	1^{9}	39^{10}	61^{11}		
	S. of 59° N.			6^{8}	12^{11}	130^{17}	174^{11}	
	Shields				18^{21}	138^{37}	269^{17}	811^{29}
1932	N. of 60° N.			35^{10}	15^{13}	88^{8}		
	59° to 60° N.			48^{18}	81^{9}	145^{21}	72^{1}	
	S. of 59° N.	5^{3}	0^{1}	—	105^{16}	71^{14}	89^{28}	1525^{6}
	Shields	3^{43}	16^{50}	64^{45}	88^{32}	—	365^{11}	72^{17}
1933	N. of 60° N.			70^{7}	17^{3}			
	59° to 60° N.		24^{9}	98^{17}	147^{5}			
	S. of 59° N.		132^{3}	574^{11}	86^{15}	117^{11}	418^{2}	228^{3}
	Shields	5^{11}	39^{40}	28^{38}	25^{25}	91^{25}	96^{28}	810^{11}

The outstanding features may be summarised as follows :—

(1) There is a general increase in abundance from north to south in all three years, which is evident also in nearly all the individual periods. The figures for the three years are as follows :—

Area.	1931.	1932.	1933.	1931–33.
N. of 60° N.	9^{28}	40^{31}	54^{10}	29^{69}
59° to 60° N.	34^{32}	96^{49}	84^{31}	75^{112}
S. of 59° N.	91^{47}	211^{68}	240^{45}	184^{160}

(2) There is a general increase in abundance through the three years, the average numbers per sample being as follows :—

	1931.	1932.	1933.
All samples	82^{112}	135^{150}	160^{87}
Samples mid-June to end July only	73^{97}	79^{109}	171^{69}

It appears that, while over the whole period the increase from 1931 to 1932 was greater than that from 1932 to 1933, over the well-sampled period mid-June to end of July the reverse is the case, the figures for 1931 and 1932 not differing to any marked extent. It is seen from the figures in (1) above that this increase in abundance occurs both N. of 60° N. and S. of 59° N., but that in the area 59° to 60° N. there is a small drop in numbers after 1932.

(3) The increase in abundance of Limacina is therefore similar to that

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* See Part II for details of the abundance of Limacina in the Shields Fishery.

of Calanus, but it is, generally speaking, less abundant than Calanus in this area over the years concerned. At the end of the season, however, as will be seen from a comparison of the tables of average figures for Calanus and Limacina, there is some evidence which suggests that the Calanus figures, which are tending to decrease to some extent, may become lower than the Limacina averages, which are tending to increase. This statement must, however, be regarded as a suggestion which cannot be confirmed on the restricted material available at this part of the season.

(4) An abnormal influx of Atlantic water into the North Sea appears to affect the Limacina population of the latter. Ogilvie (1934) says that "while there is a certain amount of carry-over of this species from one year to another the stock is annually augmented by an influx from the North which takes place from June or July onwards." In 1930 although Limacina was abundant on the West Coast, numbers were very low on the East Coast; and in 1931, with a considerable abundance on the West side, the East Coast figures were still rather low, while with a greater influx of Atlantic water in 1932 and 1933 the numbers on the East Coast increased to an appreciable extent.*

LIMACINA-HERRING CORRELATIONS.

When the material for the years 1930 and 1931 was all worked up, the correlation table for Limacina and herring, compiled from all the figures then available, showed a marked negative result (Part I, p. 160): and it was thought that this correlation might be more useful even than the Calanus one, in that it would be easier to steam out of dense concentrations of Limacina than to find the largest numbers of Calanus. When, however,

TABLE IX.

Limacina-Herring Correlation Tables.

Indices denote number of catches averaged (crans).

Limacina.	1930.	1931.	1932.	1933.	1931–33.	1930–33.
0–99	$16{\cdot}4^{46}$	$7{\cdot}1^{106}$	$14{\cdot}6^{109}$	$10{\cdot}1^{51}$	$10{\cdot}7^{266}$	$11{\cdot}6^{312}$
100–249	—	$0{\cdot}3^{6}$	$7{\cdot}9^{32}$	$11{\cdot}9^{25}$	$8{\cdot}8^{63}$	$8{\cdot}8^{63}$
250–499	—	—	$9{\cdot}0^{12}$	$10{\cdot}2^{9}$	$9{\cdot}5^{21}$	$9{\cdot}5^{21}$
500–999	—	$1{\cdot}0^{3}$	$35{\cdot}0^{2}$	$17{\cdot}0^{2}$	$15{\cdot}3^{7}$	$15{\cdot}3^{7}$
1000 and over	—	$0{\cdot}1^{2}$	$0{\cdot}0^{2}$	$7{\cdot}7^{3}$	$3{\cdot}3^{7}$	$3{\cdot}3^{7}$
or 100 and over	—	$0{\cdot}5^{11}$	$9{\cdot}0^{48}$	$11{\cdot}4^{39}$	$9{\cdot}0^{98}$	$9{\cdot}0^{98}$
% samples 100 and over	0·0%	9·4%	30·6%	43·3%		

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* There were only eight samples from the West Coast in 1932 and none in 1933, so that no information is available as to the state of the Limacina stock on the West side in these two years.

the material from the later years was also available, and subdivision in space and time was found necessary for reasons already discussed, it was seen that the results were less consistent, some being positive, and the later years less satisfactory than the earlier.

Table IX above shows the results for the years 1930 to 1933, and the combined result with and without the 1930 figures. In addition the figures for average catch in water with Limacina 100 and over are given, and the number of such catches is expressed as a percentage of the total. In 1930, with no catches in water where the Limacina figure per sample is 100 and over, there is no correlation ; in 1931 only 9·4% of the catches are in water of Limacina 100 and over, the correlation being negative for above and below this level. In 1932 the percentage of catches in water of Limacina 100 and over has increased to 30·6%, the correlation here also being negative. In 1933 43·3% of the catches are from water of Limacina 100 and over, and the correlation here for above and below 100 is slightly positive, but is neutral if the figure taken as a division is raised to 250 (Limacina 0–249—Catch 10·7^{76}, Limacina 250 and over—Catch 10·6^{14}). The figures for average catches associated with Limacina 500 and over are based on too few catches to be significant.

Table X shows the correlations obtained for the individual periods in the various areas, although these are not as numerous as the Calanus results.

TABLE X.

LIMACINA-HERRING CORRELATIONS FOR AREA-PERIODS.

Indices denote number of catches averaged (crans).

Year.	Area.	Period.	Average catch with Limacina 0–99.	Average catch with Limacina 100 and over.	Sign of Correlation.
1931	58° to 59° N.	16–31 July	1·3^{11}	1·1^{4}	–
1932	59° to 60° N.	16–30 June	25·2^{15}	13·9^{4}	–
	,, ,,	1–15 July	5·2^{7}	13·0^{2}	+
	,, ,,	16 July–1 August	28·3^{11}	17·3^{11}	–
	58° to 59° N.	16–31 July	18·6^{6}	17·0^{2}	–
	,, ,,	1–15 August	7·2^{14}	1·5^{8}	–
	56° to 58° N.	1–15 July	7·5^{6}	9·1^{6}	+
	,, ,,	16–31 July	14·4^{4}	3·4^{2}	–
	,, ,,	1–15 August	6·1^{6}	4·0^{4}	–
1933	N. of 60° N.	15–30 June	1·2^{5}	0·0^{2}	–
	59° to 60° N.	16–30 June	10·5^{12}	21·1^{7}	+
	58° to 59° N.	1–15 July	9·4^{8}	23·8^{3}	+
	,, ,,	16–31 July	1·2^{6}	7·2^{5}	+
	56° to 58° N.	16–30 June	8·5^{3}	13·7^{7}	+

This information has little real significance, there being eight area-periods showing negative correlations and six showing positive results. It should, however, be noted that four of the positive results occur in 1933. Further work may establish a reliable correlation between Limacina and herring. Our information suggests that it might be profitable to avoid really dense concentrations of this organism, but no commercial significance can reasonably be attached to the results so far obtained.

There is little evidence of correlations between the catches of herring and other zooplankton forms (see Part I, p. 159), but more extensive examination might have afforded some information of this kind.

GENERAL NOTES ON THE PLANKTON.

Zooplankton.

The abridged method of analysis adopted to economise in time affected all the material after 1931 (see Part I, p. 159), so that full information over the four years is available for a limited number of organisms only. Of these Calanus and Limacina have already been discussed in detail, leaving only the figures for Total Copepoda to be dealt with here. The figures for Total Copepoda, excluding Calanus, are shown in Table XI.

TABLE XI.

Total Copepoda (excluding Calanus): Average Numbers per Sample per Half Month.

Indices denote numbers of samples averaged.

Year.	Area.	May 16–31.	June 1–15.	June 16–30.	July 1–15.	July 16–31.	Aug. 1–15.	Aug. 16–31.
1930	N. of 60° N.		30^{5}	—	—	112^{1}		
	59° to 60° N.			43^{8}				
	S. of 59° N.					331^{4}	680^{10}	
1931	N. of 60° N.			97^{15}	24^{8}	111^{5}		
	59° to 60° N.		31^{2}	76^{9}	98^{10}	240^{11}		
	S. of 59° N.			352^{8}	360^{11}	844^{17}	1111^{11}	
1932	N. of 60° N.			621^{10}	139^{12}	455^{8}		
	59° to 60° N.			259^{18}	294^{9}	1378^{21}	2320^{1}	
	S. of 59° N.	654^{3}	1230^{1}	—	1652^{16}	1955^{14}	1410^{28}	1832^{6}
1933	N. of 60° N.			209^{7}	342^{3}			
	59° to 60° N.		2745^{9}	1122^{17}	1088^{5}			
	S. of 59° N.		785^{3}	997^{11}	504^{15}	548^{11}	317^{5}	

	Area.	1930.	1931.	1932.	1933.
Average per area in years and totals.	N. of 60° N.	43^{6}	79^{28}	384^{30}	249^{10}
	59° to 60° N.	43^{8}	136^{32}	787^{49}	1588^{31}
	S. of 59° N.	580^{14}	709^{47}	1580^{68}	625^{46}
	Whole area	312^{28}	373^{107}	1072^{147}	925^{87}

The information afforded by this table may be stated as follows :—

(1) There is an increase in abundance of Copepoda (excluding Calanus) from 1930 to 1932, and a slight drop in numbers in 1933. This is shown in

the area N. of 60° N., the drop in 1933 being small, while in the area S. of 59° N. the drop in numbers in 1933 is considerable. In the area 59° to 60° N., however, the increase is continuous from 1930 to 1933.

TABLE XII.

Zooplankton: Average Numbers per Sample per Half Month.

Indices denote number of samples averaged.

Form.	Year.	Part of area.	June 1–15.	June 16–31.	July 1–15.	July 16–31.	Aug. 1–15.	Area Av.	Year Av.
Paracalanus parvus and *Pseudocalanus elongatus*	1930	N.	0^{5}	9^{8}	—	68^{1}		10^{14}	21^{28}
		S.				74^{4}	14^{10}	31^{14}	
	1931	N.	10^{2}	37^{24}	6^{18}	15^{16}		21^{60}	41^{107}
		S.		4^{8}	28^{11}	89^{17}	113^{11}	66^{47}	
Centropages typicus and *hamatus*	1930	N.	0^{5}	0^{8}	—	0^{1}		0^{14}	141^{28}
		S.				87^{4}	360^{10}	282^{14}	
	1931	N.	1^{2}	3^{24}	15^{18}	11^{16}		9^{60}	46^{107}
		S.		18^{8}	54^{11}	110^{17}	158^{11}	93^{47}	
Temora longicornis	1930	N.	2^{5}	28^{8}	—	0^{1}		17^{14}	39^{28}
		S.				42^{4}	70^{10}	62^{14}	
	1931	N.	0^{2}	11^{24}	27^{18}	154^{16}		53^{60}	251^{107}
		S.		316^{8}	260^{11}	576^{17}	775^{11}	504^{47}	
Acartia longiremis and *clausi*	1930	N.	0^{5}	3^{8}	—	0^{1}		2^{14}	76^{28}
		S.				6^{4}	208^{10}	150^{14}	
	1931	N.	15^{2}	17^{24}	3^{18}	7^{16}		10^{60}	17^{107}
		S.		15^{8}	7^{11}	37^{17}	33^{11}	25^{47}	
Oithona	1930	N.	0^{5}	3^{8}	—	12^{1}		3^{14}	2^{28}
		S.				0^{4}	2^{10}	1^{14}	
	1931	N.	1^{2}	11^{24}	6^{18}	5^{16}		8^{60}	7^{107}
		S.		0^{8}	3^{11}	12^{17}	3^{11}	6^{47}	
Evadne	1930	N.	80^{5}	150^{8}	—	4^{1}		115^{14}	60^{28}
		S.				22^{4}	0^{10}	6^{14}	
	1931	N.	3^{2}	0^{24}	1^{18}	1^{16}		1^{60}	10^{107}
		S.		17^{8}	45^{11}	17^{17}	6^{11}	21^{47}	
Podon	1930	N.	0^{5}	0^{8}	—	24^{1}		2^{14}	4^{28}
		S.				13^{4}	4^{10}	6^{14}	
	1931	N.	8^{2}	1^{24}	1^{18}	5^{16}		2^{60}	20^{107}
		S.		2^{8}	30^{11}	59^{17}	64^{11}	44^{47}	
Lamellibranch larvæ*	1931	N.	19^{2}	10^{24}	11^{18}	5^{16}		9^{60}	7^{107}
		S.		2^{8}	9^{11}	2^{17}	3^{11}	4^{47}	
Cyphonautes larvæ*	1931	N.	41^{2}	2^{24}	72^{18}	3^{16}		25^{60}	40^{107}
		S.		37^{8}	111^{11}	31^{17}	68^{11}	60^{47}	

This increase in abundance with the passage of time is evident in most of the areas in each year, there being a general tendency to increase in abundance up to the second half of July or first half of August. The 1933 figures do not show this tendency so well, but they are not so extensive, there being little information after the middle of July.

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* Not observed in 1930. N. = Northern, S. = Southern, parts of area, 59° N. Lat. being taken as a division.

(2) There is an increase in abundance from North to South in practically all the individual periods and in the total figures up to 1932, while in 1933 the greatest abundance is in the area 59° to 60° N.

Figures for individual species of Copepods are available for 1930 and 1931 only, and those present in significant numbers are as follows:-*Paracalanus parvus* and *Pseudocalanus elongatus*, which are grouped together, *Temora longicornis*, *Centropages typicus* and *hamatus*, *Acartia longiremis* and *clausi*, and Oithona. Table XII above sets out the figures for these copepods, and other forms, for the Northern and Southern portions of the Eastern Fishery (59° N. Lat. being taken as a division).

It will be seen that, with regard to the Copepods, there is evidence of the same increase with the passage of time in the individual forms as is shown by the figures for Total Copepoda. It is noticeable also that the abundance in the southern part of the area is on the whole greater than that in the northern part. Of the other zooplankton forms, omitted from Table XII, Sagitta and the larger crustacea (e.g. Amphipods, Euphausians, and Decapod larvæ*) are scarce or absent in the Indicator samples, the numbers per sample per half-month rarely exceeding 3. The Cladocera, however, are more abundant, Evadne earlier than Podon, the latter more abundant in the southern part of the area. Lamellibranch larvæ, more abundant in the northern part, and decreasing in numbers with the passage of time; and Cyphonautes larvæ, with greater numbers in the southern part of the area and fairly high figures for 1–15 July, are found in 1931 only, no records of these forms occurring in 1930.

Phytoplankton.

The abridged method of analysis adopted for all the samples after 1931 did not affect diatoms and dinoflagellates, and the details of the Phytoplankton-Herring correlations obtained will be found in Part IV where also their commercial significance is discussed.

Diatoms are found, at times in large numbers, in all the areas of the Scottish Eastern Fishery. In 1930, however, there are only two records of diatoms (Rh.+† for two samples on the 24th July in the area 58° to 59° N.); while over the four years in the area N. of 60° N. there is only one record (Rh.+ for 20th June, 1931). For the other areas, over the years 1931–33, there are more occurrences of diatoms and these are set out in Table XIII.

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* These forms may have been considerably more abundant than our figures suggest as it is possible that they are not caught in representative numbers by the Indicator. See Part I, page 153, for fuller discussion on this point.

† See footnote to Table XIII.

TABLE XIII.

Occurrences of Diatoms.

Area.	Year.	April 16–30.	May 1–15.	May 16–31.	June 1–15.	June 16–30.	July 1–15.	July 16–31.	Aug. 1–15.
59° to 60° N.	1931				0	0	Rh.++ Ch.+ Tha.+	Rh.+ Par.+	
	1932					0	0	0	0
	1933				0	Ch.++	0		
58° to 59° N.	1931					Rh.+ Ch.+ Tha.+ N.+ Cra.+	Rh.+++ Ch.++ Tha.++ N.+	0	0
	1932						0	0	Ch.+
	1933	Ch.+++ Tha.+++ N.+++ Cosc.+			0	0	0	0	0
56° to 58° N.	1931								0
	1932			Rh.++ Ch.+++ Tha.+++ N.+++	0		Rh.++ Tha.+	0	0
	1933				0	Rh.++ Ch.+ Thx.+++ N.+++	0		0

Explanation of Symbols.

0 No diatoms recorded from samples taken.
+ Present but not exceeding 1000 cells per disc.
++ Moderately abundant, 1,000–25,000 cells per disc.
+++ Abundant, exceeding 25,000 cells per disc.
Rh. Rhizosolenia spp., Ch. Chætoceros spp., Tha. Thalassiosira spp., N. Nitzschia spp., Thx. Thalassiothrix spp., Cosc. Coscinodiscus spp., Cra. Coscinosira spp., Par. Paralia spp.

Halosphæra is recorded in the area 56° to 58° N. in 16–31 May and 1–15 June, 1932, these being the only occurrences of this form. Phæocystis is found in all the areas N. of 58° N. in the Scottish Eastern Fishery, but is not very common. It is not recorded in 1930 or 1932, and is only recorded once in 1933 (Area 58° to 59° N., 16–31 July). Most of the records of its presence refer to 1931, when it is recorded for the area N. of 60° N. in July, for the area 59° to 60° N. in 1–15 July, and for the area 58° to 59° N. for 16–30 June and July, being most abundant and occurring most often in 1–15 July. It is probable that this form was rather more widespread than these records indicate, as it is very difficult to be certain of its presence if the discs have been stored for some time before examination, but it is unlikely that any instances of its occurrence in large quantity have been missed.

Dinoflagellates are fairly abundant during the period covered by these investigations, and the figures for Ceratium species, which form the bulk of the records, are set out in Table XIV below. The numbers are given as hundreds of Ceratium and are to the nearest 100.

TABLE XIV.

DINOFLAGELLATES: CERATIUM SPECIES, IN HUNDREDS.

AVERAGE NUMBERS PER SAMPLE PER HALF MONTH.

Indices denote the number of samples averaged.

Year.	Area.	May 16–31.	June 1–15.	June 16–30.	July 1–15.	July 16–31.	August 1–15.	August 16–31.
1930	N. of 60° N.		195^{5}	—	—	0^{1}		
	59° to 60° N.			420^{8}				
	S. of 59° N.					815^{4}	71^{10}	
1931	N. of 60° N.			302^{15}	486^{8}	316^{5}		
	59° to 60° N.		530^{2}	357^{9}	192^{10}	281^{11}		
	S. of 59° N.			44^{8}	257^{11}	387^{17}	454^{11}	
1932	N. of 60° N.			514^{10}	406^{13}	1049^{8}		
	59° to 60° N.			458^{18}	605^{9}	899^{21}	1000^{1}	
	S. of 59° N.	7^{3}	678^{1}	—	276^{16}	442^{14}	503^{28}	465^{6}
1933	N. of 60° N.			804^{7}	717^{3}			
	59° to 60° N.		71^{9}	338^{17}	637^{5}			
	S. of 59° N.		2^{3}	42^{11}	315^{15}	425^{11}	567^{2}	457^{3}

	Area.	1930.	1931.	1932.	1933.
Average per area in years and totals	N. of 60° N.	162^{6}	357^{28}	607^{31}	778^{10}
	59° to 60° N.	420^{8}	290^{32}	685^{49}	308^{31}
	S. of 59° N.	283^{14}	314^{47}	415^{68}	275^{45}
	Whole area	297^{28}	318^{107}	544^{148}	345^{86}

There is, on the whole, a tendency for the abundance to be greater N. of 59° N. than to the south of this line, and for the abundance to increase to some extent with the passage of time in any one season. The general average level increases up to 1932 but drops in 1933 and only in the area N. of 60° N. do the figures increase steadily over the four years. It is possible that the 1933 season might have shown higher figures had the material been more extensive, as the figures available indicate higher numbers in the northern part of the area than at the corresponding periods in any of the previous years. The relatively limited material at the beginning of the season suggests low numbers, while there are signs of a diminution of abundance after mid-August.

THE WESTERN FISHERY.

The samples available from this section of the Scottish Fishery are restricted in both space and time, so that the few results which can be obtained may hardly be regarded as significant, except in that they afford confirmatory evidence of the Calanus-herring correlations. Few of the samples were obtained by drifters, the majority having been secured by cruisers of the Fishery Board for Scotland. (The instrument was towed close to a drifter's fleet of nets, and the catch ascertained subsequently. We are indebted to the Fishery Board for Scotland for arranging for their Fishery Cruisers to take samples for us in these waters.) Only the latter, located in the waters of the Little Minch and North Minch where they form groups on various dates, are available in sufficient numbers to form correlation tables. There are six dates when groups of samples were secured, and the results of the correlations, in terms of percentage gain or loss, are shown below in Table XV. The number of samples, five, on each of the September, 1930, dates is too small to consider these two results even as secondary results in the sense in which this term is used for the Eastern Fishery, but, for reasons given below, a combination of these two tables into one gives a misleading result, so they are quoted separately. The six sets of samples fall into three half-month periods, and these results are also shown.

TABLE XV.

ABRIDGED CORRELATION TABLES. CALANUS.

Year.	Date.	No. of samples.	Average Calanus.	Average catch. (crans)	Percentage gain or loss.	Percentage gain or loss. Half-months.
1930	22 Sept.	5	161	1·0	+ 5·3	− 72·0
	26 Sept.	5	18	5·8	+ 28·4	
1931	1 July	22	72	1·1	− 18·0	+ 5·4
	2 July	44	174	2·2	+ 7·9	
	26 Aug.	15	983	3·2	+ 27·5	+ 12·6
	27 Aug.	16	827	1·8	− 3·4	

The combination of the two September dates into one table for the half-month, which gives a loss of 72·0%, is found on examination to be unjustified. All the samples from the 22nd September fall on the higher Calanus side, and on this date a low average catch is associated with a high Calanus average (and a high Limacina average), while all the samples from the 26th September, when the Calanus average was low (Limacina also), with an increased catch, fall on the lower Calanus side. Thus the combination gives a loss, although each day indicates a gain if treated separately.

The two other half-month periods, which may more justifiably be formed from the days concerned, show gains of 5·4% and 12·6%, and average 9·0% gain, or if the individual days are used, an average gain of 3·5% is shown. (This becomes a gain of 8·0% if the two 1930 results are included.)

These results, as far as they go, provide further support for the positive Calanus-herring correlations established in the Scottish Eastern and Shields Fisheries, and indicate that increased catches would have been obtained in the Scottish Western Fishery by using the Indicator on the basis of the Calanus correlations. The average percentage gain indicated by the above results is smaller than in the other fisheries, but there are too few results to provide a reliable estimate of this figure. It should, however, be remembered that a small percentage gain in catch on a poorly supplied market may mean a relatively greater monetary return than that accruing from a greater gain when the market is well supplied; and the average catch in this fishery was low over the years concerned. The observations of Herdman and Riddell (1913) on Calanus and the herring-shoals in the Hebrides, quoted in Part I (p. 148), are of interest in considering the results for this area.

Limacina was abundant, particularly in 1931, and Table XVI shows that over half of the total samples were taken in water of over 500 Limacina per disc. Table XVI also indicates the possibility of a negative correlation between Limacina and herring, but the information is inconclusive, as in the Eastern Fishery.

TABLE XVI.

LIMACINA-HERRING CORRELATIONS.

Indices denote the number of catches averaged (crans).

Limacina.	1930.	1931.	1932.	1930–1932.
0–99	$5{\cdot}8^{5}$	$2{\cdot}5^{28}$	$1{\cdot}5^{4}$	$2{\cdot}9^{37}$
100–249	—	$0{\cdot}9^{8}$	—	$0{\cdot}9^{8}$
250–499	$2{\cdot}4^{2}$	$2{\cdot}2^{10}$	$20{\cdot}0^{2}$	$4{\cdot}8^{14}$
500–999	$0{\cdot}0^{3}$	$2{\cdot}0^{20}$	$2{\cdot}5^{2}$	$1{\cdot}8^{25}$
1000 and over	—	$2{\cdot}0^{39}$	—	$2{\cdot}0^{39}$
100 and over	$1{\cdot}0^{5}$	$1{\cdot}9^{76}$	$11{\cdot}25^{4}$	$2{\cdot}3^{85}$
0–499	$4{\cdot}8^{7}$	$2{\cdot}2^{46}$	$7{\cdot}7^{6}$	$3{\cdot}0^{59}$
500 and over	$0{\cdot}0^{3}$	$2{\cdot}0^{59}$	$2{\cdot}5^{2}$	$1{\cdot}9^{64}$

The samples available are too restricted in space and time to enable any reliable information to be obtained relating to the distribution and abundance of the plankton generally. The Calanus averages are, however, noted in Table XV.

NOTES ON SOME SAMPLES FROM IRISH WATERS.

In 1931, between the 24th of May and the 8th of June, eight samples, with associated catches of herring, were obtained from the north and west coasts of Ireland. These samples were characterised by a very great abundance of Limacina, the average being 51,866 Limacina per sample, with a maximum of 96,600 in one sample. Only one sample had less than 100 Limacina, and the associated catch was 46·0 crans, while the average for the remaining seven catches was 4·9 crans. The Calanus average was less than 100. No correlations can reasonably be drawn up for these samples, in four of which no accurate count of Calanus was obtained owing to the large numbers of Limacina present.

SUMMARY.

(1) In the Scottish Eastern and Western Fisheries 459 Plankton Indicator samples have been analysed and the results studied for evidence of correlations between the zooplankton and the 533 associated catches of herring. (See Part IV for the phytoplankton correlations.)

(2) In the Eastern Fishery, 1930–33, out of twenty half-month area-periods considered of primary value, fifteen show positive Calanus-Herring correlations and five negative. The area-periods of secondary value confirm this three to one ratio, there being eight positive and three negative results indicated. (A three to one ratio was also found in the Shields Fishery. Part II.)

(3) An attempt to estimate the commercial value of the Indicator, when used to locate the richer Calanus waters, shows that if in each period (1931–33) the fishing had taken place in the richer Calanus waters a gain of 24·5±7·7 % over the catch secured by fishing at random should have resulted.

(4) Poor catches may be secured in the richer Calanus waters and good catches in the poorer Calanus waters, but the good catches are secured more frequently in the richer Calanus waters.

(5) A seasonal fluctuation in the degree of Calanus-Herring correlation is suggested, and the irregularity at the end of the season is tentatively associated with the arrival of shoals of spawning fish.

(6) The results of the Western Fishery, although few, in general support those of the Eastern Fishery.

(7) A negative correlation between the herring and large numbers of Limacina is suggested, but the evidence is inconclusive.

(8) The abundance and distribution of Calanus, Limacina, and a number of other plankton forms are discussed.

POSTSCRIPT.

A few samples were obtained in July, 1935, by H.M.S. *Foyle*, and two correlation tables of primary value have been compiled. These samples were all taken north of lat. 59° 55′ N. and so the tables may be compared with those for the area N. of 60° N. for the earlier years.

TABLE XVII.

Summary of Data Relating to the Calanus-Herring Correlations in the Area North of 59° 55′ N. for July, 1935.

				Total catch in water of		Average catch in water of		Percentage gain or loss on total catch.
Period.	No. of samples.	Average Calanus.	Average catch.	Lower Calanus numbers.	Higher Calanus numbers.	Lower Calanus numbers.	Higher Calanus numbers.	
1–15 July	10	88	12·7	120·75	6·50	24·1	1·3	– 89·8
16–31 July	12	50	16·6	7·25	191·50	1·2	31·9	+ 92·7

Calanus reaches a higher average in 1–15 July than it did in 1931 and 1932, but is less abundant in 16–31 July than in the earlier years. Limacina is more abundant than in the corresponding periods in 1931–33, and the two correlations with this organism give negative results, supporting the suggested relation between Limacina and Herring (p. 265, also Table X).

TABLE XVIII.

Limacina-Herring Correlations.

	Average catch (crans) with	
Period.	Limacina 0–99.	Limacina 100 and over.
1–15 July	15·9^{8}	0·125^{2}
16–31 July	46·0^{4}	1·8^{8}

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Part IV. The Relation between Catches of Herring and Phytoplankton Collected by the Plankton Indicator.

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With 4 Figures in the Text.

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INTRODUCTION.

THE object of these investigations, discussed in full in Part I, is an attempt to correlate the catches of the drift-net herring fishery with the conditions in the plankton at the time of fishing, and if possible to establish useful indications as to suitable and unsuitable waters for fishing. In Parts II and III the zooplankton-herring correlations in the English and Scottish fisheries have been dealt with separately. The phytoplankton material with which this section deals is not so extensive, so that the data from both fisheries will be dealt with together. The pioneer observations of Pearcey (1885) in regard to the herring, of Bullen (1908) in regard to the mackerel, and the fact that fishermen have for long regarded what they call " weedy " or " stinking " water as a bad sign for fishing, have been referred to in Part I, page 148.

In 1922–23 Hardy (1926), making the first experiments with the Plankton Indicator in the Southern Bight, found that the catches associated with Indicator discs coloured green by phytoplankton were much lower than those with discs not so coloured. The number of records obtained was small, but the results, in support of those of Pearcey, appeared to be of considerable significance. In the autumn fishery of 1922 twelve discs were obtained with associated catches of herring. The average catch was 14·1 crans. Six of the discs were coloured green by

Phæocystis and had associated catches varying from 0·5 to 6·0 crans (av. 2·9 crans), and six discs were free of phytoplankton and had catches ranging from 15 to 45 crans (av. 25·3 crans). In March, 1923, only two records were obtained, one was green with diatoms and was associated with a catch of 1·5 crans and the other (not coloured green) was taken with a catch of 24 crans.

During the investigations carried out from Hull in 1930–33 further information has been obtained on this relationship. We have only considered those discs which were definitely green or greeny brown with phytoplankton, i.e. those which could be easily recognised as green or brown by the fishermen if using the indications as a guide to fishing. Out of 1,256 samples with the standard Indicator only 55 were definitely coloured. This was after the discs had been stored for a considerable period in formalin ; it is likely that a larger number would have been included in the category of green or brown discs if they had been examined whilst fresh, i.e. as the fishermen could have used them for indications. The small proportion of green discs may perhaps be due to several causes, (1) that the bulk of the material was collected in the summer when dense phytoplankton concentrations are rare, (2) that a very small number of samples was obtained in the autumn East Anglian fishery (see p. 282) and (3) that the fishermen, who believe that " stinking " or " weedy " water is a bad sign for fishing, will have avoided such dense phytoplankton when once aware of its presence.* In the autumn fishery of 1934 a special experiment was designed with a miniature Plankton Indicator for phytoplankton only and 150 discs were obtained of which 42 were green in colour. The results with the standard Indicator will be dealt with first.

RESULTS WITH THE STANDARD INDICATOR, 1930–33.

A list of the green or brown discs with their associated catches is shown in Table I, together with the associated numbers of *Calanus finmarchicus* (Gūnn) and *Limacina retroversa* (Flemming).† The names of the principal forms of phytoplankton are given in brackets. Table II gives a comparison between the average catches of herring associated with the green or brown discs and those with discs not so coloured, separated into half-monthly periods for the different fishing areas. Similar averages for Calanus and Limacina are also given. The 1922 and 1923 results are added. There are twenty-two periods when comparison can be made, in only four of these are the catches associated with the green discs higher than the remainder, and in three instances these are only based upon one green disc.* There appears to be no significant difference between the catches associated with Phæocystis and those associated with diatoms. The average catch of those recorded as definitely Phæocystis only, is 1·6 crans (for 13 samples), and for diatoms only, it is 2·1 crans (for 29 samples). The average catch for all the 62 green or brown discs is 1·9 crans.

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* Although occasionally dense phytoplankton concentrations may be detected at the surface, as a rule they are only evident after the nets have been shot and hauled in such conditions.

† See notes concerning these two forms on page 179 of Part II of this series.

There can be no doubt that such an indication must be reliable and valuable to the industry when it is used to save both time and money by avoiding waters in which it is highly probable that the catches will be poor.

The fact that both Calanus and Limacina also more frequently show smaller numbers in the phytoplankton regions is of considerable interest. The problem of the inter-relations between the zooplankton and the phytoplankton has been discussed at length in a recent publication by Hardy (1935). He believes that, in addition to the grazing effect of the zooplankton on the phytoplankton (cf. Harvey, 1934, and Harvey, Cooper, Lebour and Russell, 1935), there is a tendency for the smaller numbers of plankton animals to occur in regions of denser phytoplankton due to some direct or indirect excluding influence of the latter. The fact that here Limacina as well as Calanus bears a general inverse relationship to the phytoplankton would suggest support for the exclusion hypothesis, for here Limacina occurs in comparatively small numbers and so it can scarcely be regarded as controlling the phytoplankton, if indeed it is feeding on it. The question as to whether the herring avoids the phytoplankton because its food is distributed in inverse relation to it is also discussed by Hardy (loc. cit.). He believes it unlikely that such a habit, even if formed in the feeding season, would be retained in the autumn spawning season when the herring are not feeding and when the evidence shows (Savage and Hardy, 1935) that they may be deflected from, or delayed in arriving at, their collecting grounds by the phytoplankton patches. The factors underlying the relationship between the phytoplankton and marine animals are by no means fully understood as yet and a complex of different factors may contribute to the observed effects.

RESULTS WITH THE MINIATURE INDICATOR, AUTUMN, 1934.

It was considered that, while there was little doubt as to the basic fact of avoidance by herring shoals of areas of dense phytoplankton, further information should be obtained on the actual relation between catches of

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* The catches obtained during these 22 periods may be examined statistically. For each period, column 3 of Table II shows the average catch associated with the green discs whilst column 4 shows that with the non-green discs. We find that the mean catch of column 3 is only 31·6% of the sum of the means of columns 3 and 4 whilst that of column 4 is 68·4%. Thus the difference of the means is 36·8% of their sum. The Standard Error of this difference is found to be ±10·8% with a corresponding value for "t" of 3·42. There is thus a high degree of probability of the significance of this difference.

TABLE I.

List of Discs, in Areas and with Dates, Coloured Green, Pale Green, Greenish or Brownish.

		Calanus.	Limacina.	Catch (crans).
1931. Scotland West Coast.				
1st July	Diatoms (N. Ch. Th.)*	36	770	0·0
,,	,, (N. Ch. Th.)	36	2522	0·25
,,	,, (N. Ch. Th.)	36	2522	1·25
,,	,, (Sk. M.)	24	572	0·0
21st July	Phæocystis	17	1620	2·25
,,	Diatoms (Rh. spp.)	35	400	3·25
26th August	?	456	600	0·0
,,	?	456	600	1·75
1931. Scotland East Coast.				
26th June	Phæocystis	15	14	0·5
30th ,,	,, and Diatoms (Rh. spp. N.)	8	8	3·25
2nd July	,, ,, (Rh. spp.)	40	0	1·5
3rd ,,	,, and some Diatoms (Rh. spp.)	10	0	0·0
7th ,,	,,	12	0	4·0
9th ,,	? (Diatoms and possibly Phæocystis)	3	30	3·0
11th ,,	Diatoms (Th. N.)	0	8	4·0
14th ,,	Phæocystis	0	0	1·0
15th ,,	,,	0	20	1·25
16th ,,	?	0	20	1·0
17th ,,	Phæocystis	0	4	1·0
20th ,,	,,	18	10	0·5
30th ,,	,,	86	8	0·5
6th August	,,	240	48	0·0
10th ,,	?	656	72	1·0
1931. Southern Bight.				
6th October	Phæocystis	10	72	1·0
13th ,,	,,	0	0	1·0
1932. Scotland East Coast.				
27th May	Diatoms (Th.)	184	0	7·0
11th July	Phæocystis	195	125	8·0
1932. Shields.				
2nd May	Diatoms (Ch. Th. Rh. N.)	10	0	1·75
3rd ,,	Phæocystis and Diatoms (Th.)	0	0	0·25
4th ,,	Diatoms (Ch. Th. Rh. N.)	10	0	0·0
7th ,,	,, (Rh. Ch.)	108	16	3·0
8th ,,	,, (Ch. N.)	58	0	2·25
10th ,,	,, (Ch. Th.)	4	0	0·125
12th ,,	,, (Ch.)	192	8	2·5
12th ,,	Phæocystis and Diatoms (Ch.)	10	0	0·0
15th ,,	Diatoms (Th.)	80	0	10·25
15th ,,	,, (Th.)	120	0	0·0
15th ,,	,, (Th.)	24	0	0·0
16th ,,	,, and possibly Phæocystis	840	0	2·5
18th ,,	,, ,, ,,	280	0	2·5

* The letters in brackets are symbols for diatom genera, as follows: N. = *Nitzschia closterium*; Ch. = *Chætoceros* spp.; Th. = *Thallassiosira* spp.; Rh. = *Rhizosolenia* spp.; Sk. = *Skeletonema costatum* and M. = *Melosira* spp. Where the identification was doubtful due to the presence of scum and long periods of storage the sign ? is used.

TABLE I—*contd.*

		Calanus.	Limacina.	Catch (crans).
1932. Shields.				
18th May	Diatoms (N. Ch. ?)	220	0	6·0
19th ,,	,, and possibly Phæocystis	0	0	0·0
23rd ,,	,, (Ch.)	270	0	1·0
24th ,,	Phæocystis	160	0	0·0
29th ,,	Diatoms (Th.)	240	24	1·0
5th June	,, (Th.)	345	0	7·0
1932. Southern Bight.				
3rd July	Diatoms (Ch. N.)	0	0	0·2
,,	,, (Ch. N.)	0	0	0·0
1933. Scotland East Coast.				
16th April	Diatoms (Th. N.)	10	0	5·0
22nd June	,, (Th. N.)	145	65	1·0
1933. Shields.				
13th April	Diatoms (Th.) and possibly Phæocystis	1115	65	0·0
2nd June	,, (Th. Ch. Sk.)	9	0	1·0
1933. Southern Bight.				
8th June	Diatoms (N.) and Phæocystis	0	0	0·25
9th ,,	,, (Th.) ,,	0	0	0·25
15th October	,, (Rh.)	0	0	4·0

Average for all Green discs 1930, 1931, 1932, 1933 $=\frac{99\cdot075}{55}=1\cdot80^{55}$ crans.

herring and the phytoplankton. This applied particularly to the area covered by the autumn East Anglian Fishery, where phytoplankton is encountered, to a greater or lesser extent, in most years (Hardy, 1923, 1926, Savage, 1930, Savage and Hardy, 1935); and where in 1933 the influence of dense phytoplankton patches on the movements of the shoals was most marked.

Difficulty has been experienced in persuading the drifter skippers to use the standard Indicator during the autumn fishery on account of the concentration of so large a fleet of vessels and the race to secure the most suitable "berths." In addition to the time taken in towing the Indicator there is the danger of fouling the nets of other drifters. Since the sampling of the zooplankton is not of primary importance in this fishery, as the herring are not feeding at the time, Professor Hardy planned a modification of the experiment using a miniature Indicator suitable for phytoplankton indications, which could be towed by the drifter whilst the nets were being shot. A line of water could be sampled along the whole length of the fleet of nets* at a speed (although only two knots approx.) sufficient

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* The number of nets in a fleet, and therefore the length of tow, was, with a few occasional exceptions, practically constant at 91–97 in this fishery in 1934. In any case, it is considered that, even if the fleet was only of 60 nets, in concentrations of phytoplankton dense enough to affect the catches quite adequate indication would be given on this length of tow.

TABLE II.

COMPARISON OF THE AVERAGE CATCHES OF HERRING (IN CRANS) AND THE AVERAGE NUMBERS OF CALANUS AND LIMACINA CORRESPONDING TO GREEN (PHYTOPLANKTON) DISCS WITH THOSE CORRESPONDING TO OTHER DISCS. THE HIGHER OF EACH PAIR OF AVERAGES IS SHOWN IN HEAVY TYPE.

Fishery and Area.	Date.	Average herring in crans.		Average Calanus.*		Average Limacina.*	
		Green discs	Other discs.	Green discs	Other discs.	Green discs	Other discs.
	1931						
Western Scottish	July	1·14^{6}	**2·02**^{3}	31	**149**	1,401	**1,793**
,, ,,	August	0·88^{2}	**2·62**^{29}	456	**969**	**600**	230
Eastern Scottish 56°–58° N.	1–15 August	0·50^{2}	**1·64**^{7}	**448**	267	**60**	58
,, ,, 58°–59° N.	16–30 June	**1·88**^{2}	0·82^{11}	12^{2}	**42**^{8}	**11**^{2}	4^{8}
,, ,, ,,	1–15 July	1·55^{5}	**12·88**^{6}	**10**	1	6	**17**
,, ,, ,,	16–31 July	0·83^{3}	**1·32**^{12}	29	**73**	11	**178**
,, ,, 59°–60° N.	1–15 July	**3·00**^{1}	1·83^{9}	3	**91**	30	**40**
,, ,, N. of 60°	1–15 July	4·00^{1}	**16·96**^{7}	12	**54**	0	**2**
,, ,, ,,	15–31 July	0·50^{1}	**0·81**^{4}	18	**112**	**10**	4
Humber	October	1·00^{2}	**39·2**^{5}	5	**49**	36	**625**
	1932						
Eastern Scottish 56°–58° N.	16–31 May	7·0^{1}	**25·75**^{2}	184	**676**	0	**8**
,, ,, ,,	1–15 July	8·0^{1}	**8·36**^{11}	195	**224**	125	**128**
Shields	1–15 May	1·83^{11}	**3·0**^{5}	56	**506**	2	**3**
,,	16–31 May	1·86^{7}	**3·8**^{36}	287	**501**	3	3
,,	1–15 June	**7·0**^{1}	4·07^{49}	345	**875**	0	**16**
East Anglian	3 July	0·1^{2}	†	0	†	0	†
	1933						
Eastern Scottish 56°–58° N.	16–30 June	1·0^{1}	**13·4**^{9}	145	**421**	65	**663**
,, ,, 58°–59° N.	16–30 April	5·0^{1}	†	10	†	0	†
Shields	13–30 April	0·0^{1}	**3·0**^{2}	**1,115**	1,080	**65**	20
,,	1–15 June	1·0^{1}	**2·09**^{39}	9	**205**	0	**20**
East Anglian	1–15 June	0·25^{2}	**2·0**^{1}	0	**1**	0	0
,, ,,	1–17 October	**4·0**^{1}	0·0^{2}	0	**20**	0	**30**
	1922–23						
East Anglian	Oct.–Nov. (1922)	2·92^{6}	**25·33**^{6}	—	—	—	—
,, ,,	March (1923)	1·5^{1}	**24·0**^{1}	—	—	—	—
Frequency of higher averages		4	18	3	17	5	13

The Indices denote the number of samples on which the average is based.

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* In these columns the averages are based on the same number of samples as in columns 1 and 2 excepting the period 16–30 June, 1931 (Area 58°–59° N.), when 13 catches were associated with only 10 samples of plankton.

† During these periods there were no other samples to compare with the green discs.

to sample the phytoplankton. The Indicator was similar in design to the standard instrument described in Part I, but only 13 inches in length and

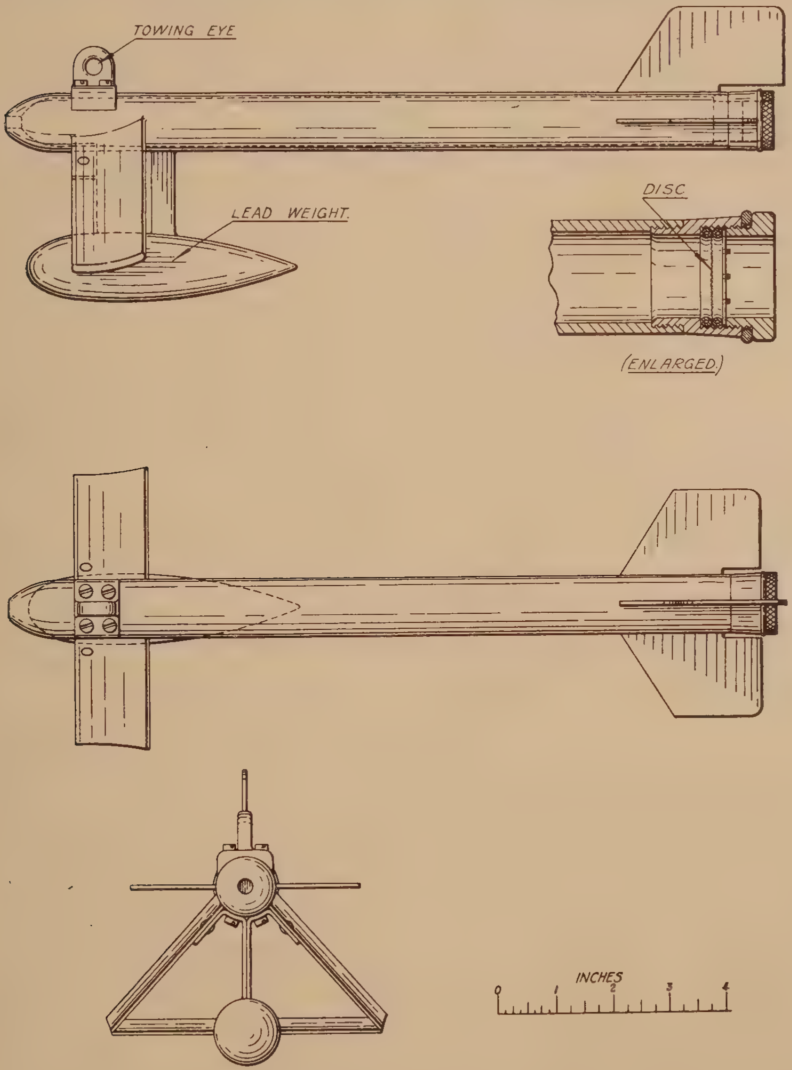

Fig. 1.—The miniature Plankton Indicator designed for sampling phytoplankton.

1 inch in diameter, with additional planes placed at a marked inverted dihedral angle to give the necessary stability and sinking effect to so small an instrument. This miniature Indicator is illustrated in Fig. 1.

It was necessary that the discs should be worked up immediately in the fresh condition, so that their colour would not be changed by long immersion in preservative, as almost certainly occurred with some of the earlier material; and also it was most important that the amount of work required from the fishermen using the instrument should be reduced to the absolute minimum. Each of the writers at different times took part in the work of collecting and examining the discs.

The method adopted was as follows :—A number of the small Plankton Indicators ready loaded with discs were issued to skippers of drifters working from Yarmouth, who were requested to shoot the instrument from the port quarter* when commencing to shoot their nets, allow it to tow at the full length of line supplied (6 fathoms) till they had finished shooting their gear, then haul it in and put it safely aside till they returned to port next morning. Details of catch, position, time, etc., were obtained and noted by the worker, who reloaded the instrument ready for the next haul. The used disc was wrapped up temporarily in a piece of damp calico, and examined later in the day when all the drifters had been visited.

Twenty-five of these small Indicators were in use, and a total of 150 samples was obtained between 7th October and 20th November, the period of maximum productivity in the fishery. The distribution of these samples is shown in Fig. 2. The total would have been greater had the market conditions not been in such a chaotic state, for there were times when less than a third of the fleet working from Yarmouth was at sea (and therefore probably only six or eight indicators), and on two occasions fishing operations were entirely suspended for several days owing to glutting of the market. This was unfortunate, as it reduced considerably the number of samples which could be obtained on any one day.

In view of these interruptions in fishing, and since the distribution of the samples is irregular in space, we decided to arrange the samples into groups of not less than six and extending over 1, 2, 3 or 4 days, so reducing gaps in the time sequence when samples were not available. There are 15 such groups varying from six to seventeen samples.

It seems very probable that the phytoplankton was not so abundant in this area in 1934 as it was in 1933, and less than one-third of the discs obtained were visibly coloured by diatoms or flagellates. In all 42 discs were obtained which could be described as visibly green or greeny brown in colour. The average catches associated with such discs have been compared with the catches of those not so coloured, but a further correlation has been made, based on the actual numbers of phytoplankton cells

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* The vertical rudder on the indicator was bent a little to make the instrument sheer out a bit on the port quarter and so tow well clear of the nets, which are shot over the starboard side. In only three hauls out of 150 was any damage to nets experienced, and in two of these cases the damage was slight.

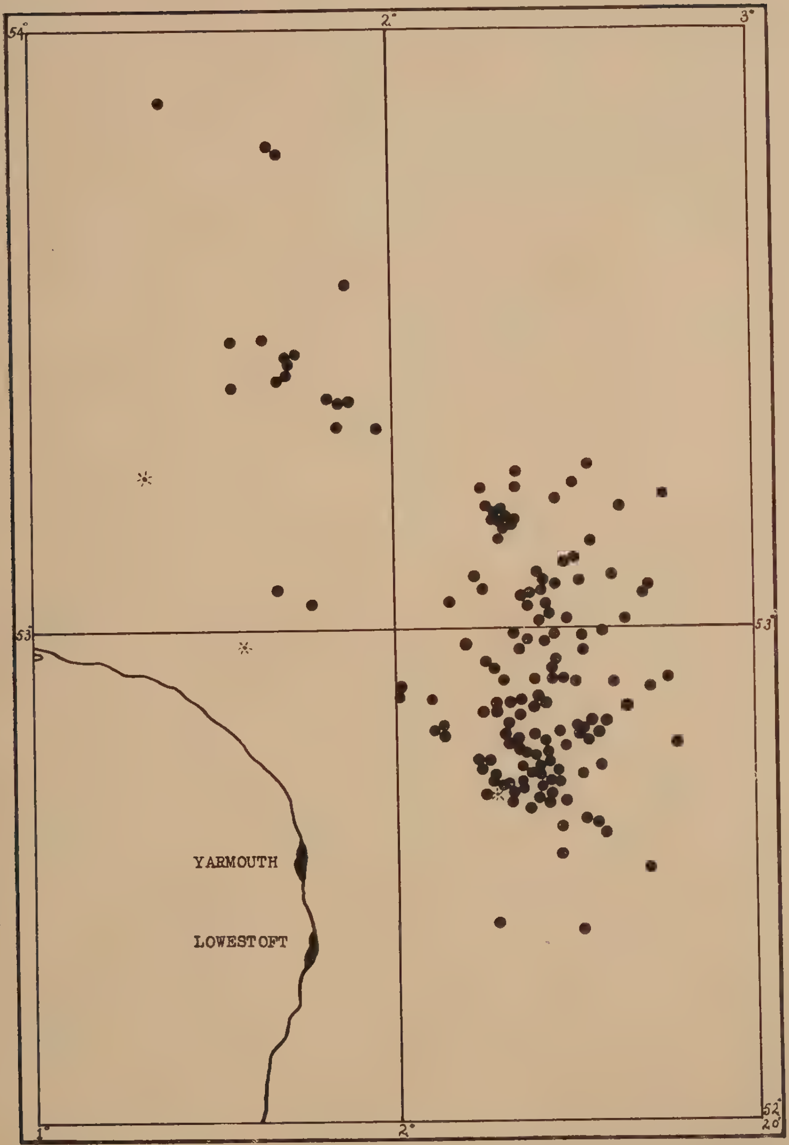
54°
2°
3°
53°
53°
YARMOUTH
LOWESTOFT
1°
2°
52°
20'

FIG. 2.—Chart showing the distribution of phytoplankton samples obtained with the miniature Plankton Indicator in the autumn East Anglian fishery, 1934. Light vessels are indicated thus *.

present. The principal forms found were *Rhizosolenia styliformis*, ranging from 0–2280 cells, and *Biddulphia sinensis* and *mobiliensis*, ranging from 0–2314 cells and composed almost entirely of *B. sinensis*.

Other diatoms were present on occasion, but seldom in appreciable numbers. *Chætoceros* spp. and *Bellarochia malleus* were the commonest of these, but as their cells are so much smaller than those of Rhizosolenia and Biddulphia they can safely be omitted from the correlations. Phæocystis and Halosphæra were found on a few discs, sometimes abundant enough to colour the disc.

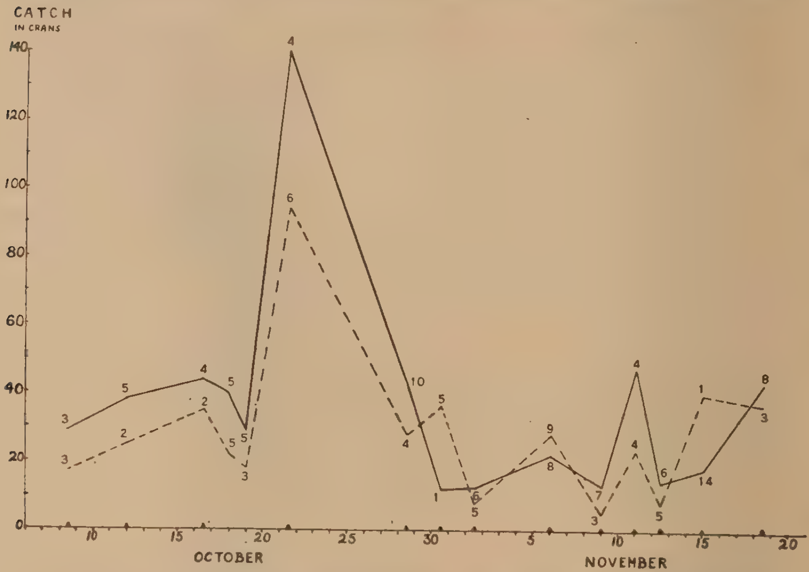

FIG. 3.—The average catch of herring associated with miniature Indicator discs having little phytoplankton (points connected by continuous line) compared with the average catch associated with discs having abundant phytoplankton (points connected by broken line) for thirteen short periods during the autumn East Anglian fishery of 1934. The figures against the graphs indicate the number of catches averaged. For details of phytoplankton measurement and length of periods chosen see text.

It was decided to divide the samples into lower and higher phytoplankton values: the lower values having less than 50 cells of Rhizosolenia plus Biddulphia, no Phæocystis, and Halosphæra not causing visible green coloration when present, and the higher values having more than 50 cells of Rhizosolenia plus Biddulphia and (or) Phæocystis present and (or) Halosphæra present and causing visible green coloration. There were 90 samples in the lower phytoplankton category and 60 in the higher. The average catches for each of these categories corresponding to each short period, are shown in Table III, columns 1 and 2; columns 3 and 4 show the average catches of uncoloured and coloured discs for the same periods. Column 5 shows the average landings at the port for the same periods. The results are also shown graphically in Figs. 3 and 4. The table shows that 12 out of 15 periods suggest that lower catches of herring are to be associated with higher phytoplankton values. Only one of the three positive correlations is seriously opposed to this general tendency (i.e. on 5–7 November), the others having only one catch on the lower or the higher side of the correlation. Such a result is interesting in itself as giving a very clear demonstration of the avoidance of phytoplankton by

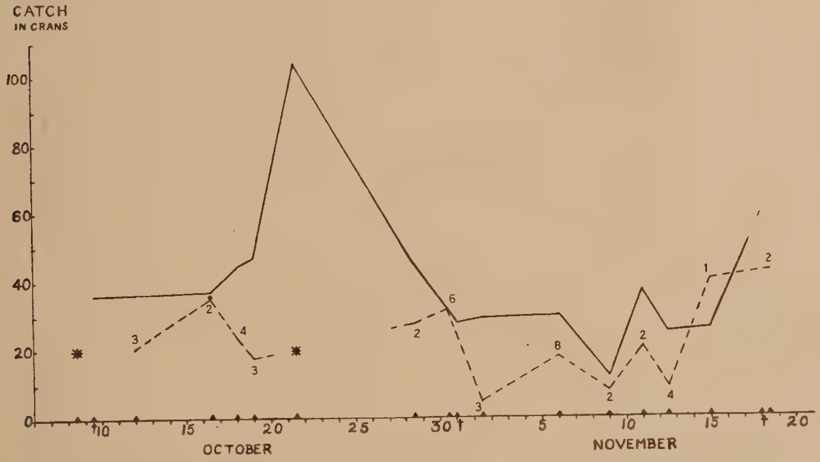

FIG. 4.—The average catch of herring associated with miniature Indicator discs which are coloured green (points connected by broken line) compared with the average landings at Yarmouth (points connected by continuous line) for the periods used in Fig. 3. In the two periods marked by an asterisk no green discs were taken. For the three periods marked by a dagger the dates for the port averages differ slightly from those used for the disc groups (see Table III, col. 6).

the herring, even though the patches are not very dense. Of the 60 samples having the denser phytoplankton, 42 were visibly coloured green or greeny brown, i.e. distinguishable from the other discs by the naked eye: columns 3 and 4 show how the associated herring catches are definitely lower when the sample is coloured than when it is not. Only two of these correlations are positive, and to some extent this arrangement explains the positive results in the previous correlations: that on the 30–31 October is explained by the fact that all the discs were green and on the 5–7 November the positive correlation based on numbers becomes negative on a colour basis. The results on the 14–16 November are similar in both sets, only one green disc being obtained; the last result having only two green discs is slightly positive, whereas it was negative in the previous correlations. Thus in only two of the periods do the greenish discs show a positive tendency. As a whole the coloured discs are associated with lower catches than those having merely the higher numbers of phytoplankton ; the results from coloured discs are also on the whole more consistently negative.*

It will be seen in column 4 of Table III that even where the discs were coloured the associated catches were sometimes quite appreciable (the average of all coloured discs being 21^{42} crans). Comparison with page 281 shows that this average is very much higher than the average (1·80 crans) of the green discs collected by the larger Indicator over the whole of the area under investigation. The following factors may help to account for this : (1) Phytoplankton was relatively sparse over the fishing area in 1934. (2) The average catch in the East Anglian fishery is in a general way very much higher than the average in the other fisheries ; thus the average of the catches associated with the samples obtained in 1934 was

TABLE III.

For explanation, see text.

	Average catch of Herrings in Crans.				
Date.	Lower phyto-plankton.	Higher phyto-plankton.	Plain discs.	Green or brown discs.	Av. catch at Port.
October					
7–10	**29^{3}**	17^{3}	No coloured discs		36 (Av. for week ending 13th)
11–13	**38^{5}**	25^{2}	**45^{4}**	20^{3}	
16–17	**44^{4}**	35^{2}	**44^{4}**	35^{2}	37
18	**40^{5}**	22^{5}	**36^{6}**	24^{4}	44
19	**29^{5}**	18^{3}	**29^{5}**	18^{3}	47
21–22	**140^{4}**	94^{6}	No coloured discs		104
28–29	**43^{10}**	28^{4}	**41^{12}**	$27\frac{1}{2}{}^{2}$	45
30–31	12^{1}	**36^{5}**	—	$31\frac{1}{2}{}^{6}$	28 (31st)
November					
1–2	**$12\frac{1}{2}{}^{6}$**	8^{5}	**$12\frac{1}{2}{}^{8}$**	5^{3}	29
5–7	22^{8}	**28^{9}**	**31^{9}**	18^{8}	30
8–10	**13^{7}**	5^{3}	**11^{8}**	8^{2}	12
11	**47^{4}**	23^{4}	**$39\frac{1}{2}{}^{6}$**	$20\frac{1}{2}{}^{2}$	37
12–13	**14^{6}**	8^{5}	**13^{7}**	9^{4}	25
14–16	18^{14}	**40^{1}**	18^{14}	**40^{1}**	26
17–20	**43^{8}**	37^{3}	41^{9}	**$42\frac{1}{2}{}^{2}$**	59 (17th, 18th, 19th)

Index figures indicate the number of samples on which the figure is based.

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* We can examine these data statistically as in the previous example quoted on page 279. Comparing the mean catches associated with the lower and higher phytoplankton numbers (see above) we find a difference of 12·6% of the sum of the mean catches obtained under both conditions (Standard Error of ±6·79%). For the mean catches of the green and non-green discs there is a difference of 17·4±6·06%, and the catches associated with the green discs compared with the average catches landed at the port show a difference of 23·6±6·57%. In each example the catches associated with the denser phytoplankton were the lower. The corresponding values for "t" are 1·86, 2·86 and 3·63.

32 crans (for 150 samples) whereas the average catch associated with all the samples taken in 1930–33 was 10 crans (1,256 samples). (3) The discs labelled green in the 1930–33 tests, after some period of immersion in formalin, would undoubtedly be the densest of a larger number which may have appeared green whilst fresh ; we feel that these would tend to be associated with a rather lower average catch than that of the fresh green discs.

These results as a whole suggest that the discs obtained with the small Indicator could be used with advantage by fishermen in avoiding the less profitable waters ; any green coloration could be observed easily by fishermen using the instrument. The 1934 material offers substantial support to the more scattered information obtained in 1930–33 in various fisheries round the British coast, and points to the value of the Indicator as a commercial instrument. There is no doubt that the miniature Indicator, so readily hauled inboard, could, in the autumn fishery, be easily used without risk of damaging the nets of other vessels and such an instrument might usefully be issued as an auxilliary to the standard Indicator.

Dinoflagellates.

The correlations which have been dealt with above have all been concerned with diatoms or green flagellates. A large amount of dinoflagellate material has been collected in the course of the five years, and we tried to find whether the abundance of dinoflagellates (mainly Ceratium spp.) could be correlated with the catches of herring. In 1931, off the Shields coast, there seemed to be a definite negative association between dinoflagellates and herring catches, but in Scottish waters this appeared to be reversed in 1932. These were the dominant years for these areas ; in the other years the dinoflagellates were relatively scarce, though in 1933 they were much more abundant in Scottish than in the English waters and on the whole the higher numbers in the Scottish areas indicated lower catches. We have not found any definite and continuous correlation as with the other phytoplankton, but perhaps this is not remarkable, considering the differences in metabolism between these forms.

Acknowledgements.

The writers wish to express their appreciation of the assistance they have received in carrying out this work ; in particular to the Humber Pilots, who provided facilities for the preliminary tests of the small Plankton Indicator, to Messrs. Bloomfield's Ltd. of Great Yarmouth, who very kindly provided accommodation and facilities for laboratory work, to the skippers of the drifters collecting the material, without whose ready and willing co-operation the work could not have been carried out, and to the officials of the Ministry of Agriculture and Fisheries who provided details of the daily landings at the port and the progress of the fishery.

SUMMARY.

1. An analysis is made of the catches of drift-net herring and associated samples of phytoplankton collected with the standard Hardy Plankton Indicator and also with a miniature form of this instrument.

2. Fifty-five green discs and their associated catches obtained off the east and west coasts of Scotland, off Shields and the East Anglian coast during the years 1930–33 are compared with the other catches in these waters period by period. The results strongly suggest a negative correlation between the herring and dense patches of phytoplankton.

3. A more detailed investigation of the autumn East Anglian herring fishery in 1934 with the miniature Indicator produced similar results and shows how such a miniature instrument should be of use in these waters, enabling fishermen to avoid unsuitable waters for fishing.

4. The correlation between the phytoplankton and the associated numbers of Calanus and Limacina is shown to be negative for each of these animals. The significance of this is discussed.

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On the Association of Jelly-fish and other Organisms with Catches of Herring.

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INTRODUCTION.

INVESTIGATIONS into the relations between plankton and herring, using the Hardy Plankton Indicator, were carried out by this department during the years 1930 to 1933 (Hardy, Henderson, Lucas and Fraser, 1936). In planning this work Professor Hardy made provision for obtaining information, when possible, on weather conditions and on the occurrence of organisms which would not be caught in the plankton samples. Information on the presence of jelly-fish was specifically requested. Skippers of drifters using the Indicator were asked to fill in a printed label for each disc giving details of ship, date, time, position and catch, and the following sentence was printed at the foot of the label :—" Any further notes regarding state of weather, sea, presence of jelly-fish, or any unusual conditions may be written on the back."* Since the details of date, position, catch, etc., were essential for the success of the Indicator experiments, only these were definitely asked for, and skippers were left to supply further information if they had time to do so. Much more exact and extensive information regarding the presence of jelly-fish and other organisms could have been obtained if the enquiry had been confined to these points, and it is hoped that this may be done in the future, either from this department or by other workers. Russell (1935, b), in stressing the importance of plankton organisms as indicators of different hydrological conditions, says " it is especially valuable to watch for any correlations between the presence or absence of certain plankton animals with that of fish and larger swimming animals." Our records, although not very extensive, are put forward as a contribution to this subject.

Russell (1935, a) has noted the close association between *Cosmetira pilosella* and *Sagitta elegans* in the waters off Plymouth. He concludes that both (together with other forms) are brought into this area by " western " water at times when a decreased flow of Atlantic water into the northern North Sea permits an increased flow of Channel water through the Straits of Dover. These forms (with others) are taken to be "indicators" of "western" or warm Atlantic water. The disturbing effects of Atlantic water on herring fisheries have previously been commented upon (Bowman, 1922, and Hardy, 1922). Savage (1926) suggests that small medusæ (as *Obelia*, *Bougainvillea britannica*, *Phialidium hæmisphæricum* and *Lizzia blondina*) "may react in a similar manner to *Phæocystis* when very abundant, but this is only a tentative suggestion." Again, it is not uncommon to hear drift fishermen associate poor catches with abundance of jelly-fish on the fishing grounds. In particular we may quote from *The Fish Trades Gazette* (22nd June, 1935) at the time of the collapse of the spring herring fishery at Shields in 1935. "The fishermen say there are swarms of small jelly-fish in the sea on the usual fishing grounds." The Report of the Scottish Fishery Board for 1931 (1932, p. 65) mentions large numbers of medusæ (*Laodicea*, *Tiaropsis*, *Cosmetira*, *Mitrocoma*, *Thaumantias* and *Obelia*) as occurring in association with the squid *Ommatostrephes*, which was particularly abundant at the time of the breakdown of the Shetland herring fishery in 1931. Hjort (1912) refers to *Ommatostrephes todarus* pursuing the herring on the Norwegian coast. "They generally appear in enormous shoals, coming from the open ocean in pursuit of the herring shoals on which they gorge themselves greedily." The squid can be caught with herring as bait and they are in turn stored as bait for the cod fisheries. Dog-fish are often mentioned by fishermen as the causes of low catches even when herring are fairly abundant in the area, and whales and sharks possibly have a similar effect.

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* These notes refer to conditions at the time of taking the sample and during the time that the gear was shot.

JELLY-FISH.

Of the 132 references to jelly-fish, 18 have the remark "No jelly-fish," and these have been omitted from consideration here, as there must have been many occasions when this statement *could* have been made, but was not. Of the remaining 114, some are indefinite as to type or quantity, but usually some expression is given of quantity, such as "few," "many" or "very many" and often brief notes of colour, size or type are added.

We may conveniently divide the records into a number of categories and will begin with those labelled "small." In each category we will give the catch associated with each particular label and with it also the average landing at the port, when that is available, for the weekly period in which the sample was taken. It will be realised that this is only of limited value since "jelly-fish" may have also been associated with many of the catches that go to make up this average but of which we have no record. The figure is given as a guide to whether the catch concerned is a high or a low one compared with the average of the fishery at the time.

Small jelly-fish are noted on twenty-two occasions. Eight of these may be classified as "few small," but one of these requires separation and special comment. The records of the seven remaining "few small" are tabulated in Table I, where we see that these figures in themselves are insufficient to provide any reliable results. The one example separated from the rest is of interest in relation to the records which follow: it is from the Shields area (20.6.33) and gave a catch of 20 crans (port average of 6·2 crans). The label reads "Few small *white* jelly-fish in the first five nets and no herring in them." This record is separated from the other seven because the 20-cran catch was taken *outside* the zone of small *white* jelly-fish. The possible significance of colour will be discussed when we have compared the data for the "many small" with the "few small" just recorded.

TABLE I.

RECORDS RELATING TO "FEW SMALL JELLY-FISH."

Date.	Area.	Remarks on label.	Catch.	Av. catch at port for week.
5.6.33	Shields	Few small *white** jelly-fish	0·5	4·3
11.6.33	,,	,, ,, *white* jelly-fish	1·0	2·8
17.9.31	E. Anglia	Several small blue jellies	5·0	20·9†
24.7.31	E. Scottish	A few squid and small jellies	5·5	2·8
20.7.32	,,	,, small jellies	9·75	17·4
27.8.31	Shields	Few small jellies	14·0	6·5
12.6.32	E. Scottish	A few small blue jelly-fish	18·0	7·9

* The word *white* is italicised throughout for ready reference.

† Average of catches associated with Indicator discs.

There are eleven records of "many small," two of which may be separated for special consideration. The remaining nine records are tabulated in Table II.

TABLE II.

RECORDS RELATING TO "MANY SMALL" JELLY-FISH.

Date.	Area.	Remarks on label.	Catch.	Av. catch at port for week.
5.6.33	Shields	Large quantities of small *white* jellies	0·0	4·3
10.6.33	,,	Water in this area was full of small *white* jellies	0·0	2·8
28.9.33	E. Anglia	Many small *white* jellies when hauling	0·0	24·4*
23.6.32	W. Scottish	Large quantities of small *white* jelly-fish	0·0	2·5
28.6.32	,,	Still getting large quantities of small *white* jellies	0·5	3·0
10.7.31	Shields	Large numbers of small *white* jelly-fish. All drifters in 5-mile radius in all directions practically blank. All report small *white* jelly-fish	1·0	16·4
20.8.31	,,	Large numbers of small jellies	2·0	7·1
19.7.33	E. Scottish	Many small blue jellies in water here	2·0	4·2
17.6.31	,,	Large number of small brown jellies	5·0	9·1

* Having no port averages for this area, the average for the month of the remaining disc catches has been used.

We see that in each instance the catch associated with "many small" jelly-fish is low and also considerably smaller than the port average. The catches are particularly small in relation to the "many small *white*" jelly-fish. This was also the case in the examples of even a "few small *white*" (see Table I and the special example in text), but as noted later there is one record labelled "small *white* jellies" with no indication of quantity, which has an associated catch of 35 crans. The two examples separated from Table II, together with that for July 10th, 1931, given in the Table, are of particular interest. From the Shields area (22.6.33) came the following note with an associated catch of 2 crans (average at the port 6·2 crans).

> "Hauled 70 nets and got no herring at all, as they were full of small *white* jelly-fish, but the last 27 nets were clear of them and that was where we got the two crans of herring."

The second separated example is from the Eastern Scottish fishery (18.7.33) associated with a catch of 6 crans (port average 4·2 crans).

> "Many small *white* jellies in the water and nets at hauling time. These jellies went down (?) towards daylight and we found the six crans in those nets hauled after this time."

In each case, as in the one previously cited, the herring were taken outside the zone where the small *white* jelly-fish were visible. In the last example the skipper queries his remark "down." As a drifter hauls her nets, she moves slowly through the water and it is possible that she passed out of the zone of jelly-fish into a region clear of them where the six crans were taken.

The evidence suggests that "many small" jelly-fish, particularly "many small *white*" jelly-fish, are indications of poor catches. This receives further support from a comparison of the average of the catches associated with "few small" jelly-fish, "many small" jelly-fish and "many small *white*" jelly-fish respectively.

Average catch with "few small" jelly-fish =9·3 crans (8 samples)
,, ,, ,, "many small" jelly-fish =1·7 ,, (11 samples)
,, ,, ,, "many small *white*" jelly-fish=1·2 ,, (8 samples)

There are three records of small jelly-fish with no indication of quantity; they are as follows:—

Date.	Area.	Remarks on label.	Catch.	Av. catch at port for week.
23.6.31	E. Scottish	Small *white* jellies	35·0	19·6
16.9.31	E. Anglian	Small blue jellies and occasionally a large one	0·25	20·9
8.7.32	E. Scottish	Small berry-like jellies*	9·5	15·4

* See p. 298.

There are seven records in which the notes refer to "many large" jelly-fish being present, all of which were recorded off Shields in July, 1931. These are given in Table III. In two instances the catch is approximately equal to that of the port, in two it is lower than the port average, and in three it is higher than the average. There is one other record of "large" jelly-fish included in the category of "stinging" jelly-fish.

TABLE III.

Records Relating to "Large" Jelly-fish in the Shields Fishery, July, 1931.

Date.	Remarks on label.	Catch.	Av. catch at port for week.
July 6	Large numbers of large jelly-fish	7·0	16·4
July 27	,, ,, ,, ,,	11·0	17·1
July 11	,, quantities of large jelly-fish	17·0	16·4
July 24	,, numbers of large jelly-fish	20·0	20·4
July 16	,, quantities of large brown jelly-fish	35·0	15·2
July 20	,, ,, ,, jelly-fish	41·0	20·4
July 18	,, numbers of large jelly-fish	48·0	15·2

We may next take those labelled in regard to colour but not size; these are given in Table IV. Here we see that in ten samples out of twelve the average at the port was higher than the catches associated with the jelly-fish.

TABLE IV.

Records giving Colour Notes Relating to Jelly-fish but no Indication of Size.

Date.	Area.	Remarks on label.	Catch.	Av. catch at port for week.
6.7.32	Shields	Large quantities of *white* jellies	3·0	6·0
12.5.32	,,	Few *white* jellies	0·0	4·3
11.7.32	E. Scottish	1 or 2 blue jellies	10·0	11·9
15.7.32	,,	Blue jellies	9·0	11·9
18.7.32	,,	,, ,,	7·0	11·9
19.7.32	,,	,, ,,	1·0	11·9
20.7.32	,,	Several blue and brown jellies	5·5	11·9
2.7.31	,,	Brown and blue jellies	0·5	16·0
21.7.31	,,	Blue and brown jellies	0·25	1·4
19.6.31	,,	,, ,, ,,	8·0	9·1
18.6.31	,,	,, ,, ,,	20·0	9·1
20.6.31	,,	,, ,, ,,	32·0	9·1

In Table V there are ten records of "stinging" jelly-fish, the whole averaging 9·4 crans, and the catches ranging from 0·0 to 32·0 crans. There are one or two points in connection with these which are of interest.

The five records between June 30th and July 31st are from Scottish waters (area 58°–59° N.) and the catches averaged 3·7 crans (all being less than the corresponding port averages); of these, three low catches were associated with dense patches of diatoms (marked †) or Phæocystis (marked *) which may account to some extent for the low average compared with the remainder of these records. In 1932 there was only one record, on July 14th, with a catch of 9 crans. The remaining four records are in the Shields area during the first half of August, 1933, and they have an average catch of 16·8 crans: these and the 1932 Scottish catch were all higher than the port averages. The Scottish records in 1931 are all from the same observer, and it may be reasonable to deduce that they refer only to one type of jelly-fish. A note attached to one runs as follows: "Stinging jellies. Alongside of ship are countless numbers of minute fish. Caught some in basket. They were adhering to jelly-fish. Gear full of evil-smelling, greenish-coloured slime." These fish were sent to the laboratory together with the disc, and were found to be young *Gadus merlangus*: it seems possible that the medusæ were Cyanea, commonly found in association with young whiting (Russell, 1931). The disc was covered with Phæocystis, and some diatoms were also recorded.

TABLE V.

Records Relating to "Stinging" or "Burning" Jelly-fish.

Date.	Area.	Remarks on label.	Catch.	Av. catch at port for week.
3.7.31	E. Scottish	Stinging jellies. Alongside of ship are countless numbers of minute fish. Caught some in basket. They were adhering to jelly-fish. Gear full of evil-smelling, greenish-coloured slime.*†	0·0	15·2
30.7.31	,,	A few stinging jellies. . . . Water very clean. There were catches here to-night up to 90 crans. Herring very spotty	0·125	2·9
2.7.31	,,	Stinging jelly-fish. Also nasty dirty yellowish substance.*†	1·5	15·2
30.6.31	,,	Jelly-fish of the stinging and burning variety.†	3·25	15·2
1.7.31	,,	Stinging jelly-fish in abundance. Several catches up to 50 crans caught in near vicinity	13·5	15·2
14.7.32	,,	A few jellies, burning and others	9·0	7·0
3.8.33	Shields	A few stinging jellies	8·0	4·7
7.8.33	,,	A lot of stinging jelly-fish	12·0	4·7
6.8.33	,,	A few stinging jellies	15·0	4·7
8.8.33	,,	A few big stinging jelly-fish	32·0	4·7

A "cut crystal" variety of jelly-fish is mentioned twice, with associated catches of 1 and 11½ crans: on the second of these a note is added, "Herring never are plentiful amongst these." "Small berry-like jellies" (possibly Pleurobrachia) are recorded once, with a catch of

*† See text.

$9\frac{1}{2}$ crans. (The catches associated with these three discs are all less than the corresponding port averages.)

In addition to the records already dealt with, there are fifty* in which quantity only is recorded: these are shown in Table VI, together with their corresponding port averages. Although described under various headings, broadly they can be grouped under the heads of "many" or "few" jelly-fish. The figures are as follows:—

	Scotland.	England.	Total.
Average catch with "many" jelly-fish	9·6(10)	12·3(29)	11·6(39)
,, ,, ,, "few" jelly-fish	15·3(5)	18·1(6)	16·8(11)

(The figures in brackets denote the number of catches averaged.) Thus, as far as we can place reliance on this type of comparison, we see that there is a consistency in the relations of the catches associated with "many" and "few" jelly-fish. Their relation with the corresponding catches at the port is shown below.

Area.	Category.	Number of samples.	No. in which port average is higher.	No. in which port average is lower.
Scotland	Many	10	6	4
,,	Few	5	3	2
England	Many	29	19	10
,,	Few	6	5	1
Total S. and E.	Many	39	25	14
,, ,,	Few	11	8	3
Grand total		50	33	17

In each category we see that the port average is more often higher than that of the catches associated with jelly-fish than lower.

The information regarding jelly-fish put forward here can only be considered as a tentative beginning to a more extensive accumulation of data which it is hoped may be built up in the future by different workers. It does suggest that a definite negative relation exists between the herring and an abundance of "small jelly-fish" and particularly the "small *white* jelly-fish." This relationship may extend beyond these categories, but we must bear in mind the possibility of different types of jelly-fish bearing different relationships to the herring. The term jelly-fish may, in any of the waters investigated, refer to medusæ or ctenophores, and in the Scottish waters it is not impossible that salps or doliolids may be referred to (Bowman, in 1922, associated an influx of salps with the poor herring fishing of 1921). The indications revealed here would appear to warrant further researches and it is in the hope that further interest may be aroused in this problem (see also Russell, 1935, b) that we publish these scanty data.

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* Eleven other records mention jelly-fish but give no further details, the catches ranging from 0·0 to 28·0 crans, and averaging 7·3 crans.

The bulk of the data refers to 1931, and it seems possible that this year was characterised by a greater abundance of " jelly-fish," visible on the fishing grounds generally, than the years 1932 and 1933.

SQUID.

The Report of the Scottish Fishery Board for 1931 (1932) refers to the occurrence in 1930* of the squid *Ommatostrephes sagittatus* whose " appearance in large numbers on the drift-net grounds was almost synchronous with the sudden and complete break in the drift-net fishery."† They were again abundant on the grounds in 1931, but further south. In 1932‡ they were reported as being neither troublesome nor numerous.

With the exception of two between Lats. 59°–60° N. our records associated with squid were obtained in the area between Lats. 58° and 59° N. and between June 30th and July 30th, 1931 ; the average catch was $1{\cdot}5^{14}$ crans. The average for all our samples in that area in July was $4{\cdot}0^{26}$ crans. Of the sixteen samples, thirteen are fairly definite as to quantity and three are vague : they are listed in Table VII. Five catches noting " few squid " averaged $10{\cdot}6^{5}$ crans : four noting " some squid " averaged $1{\cdot}0^{4}$ crans, and four noting " many squid " averaged $0{\cdot}5^{4}$ crans. Of the 16 catches, 13 were lower than the corresponding weekly port averages. This scanty material suggests a negative correlation between squid and herring catches.

DOGFISH, WHALES AND SHARKS.

The Report of the Scottish Fishery Board for 1930 (1931, p. 21) refers to fishermen on the West Coast being troubled with basking sharks, dogfish and other pests. In 1931 we received a brief report from a skipper who had taken samples for us in late June and July off the Scottish coast. Part of this runs, " Squids, dogs and foul marine growth all were too numerous in the northern waters this season. Especially the east sides of Orkneys and Shetlands. On the west side of Orkneys and the north-west side of Scotland there were no squids. Dogs there always are and only a few jellies."

There seems to be a general consensus of opinion among fishermen that whales, sharks and particularly dog-fish, cause considerable harm by driving the herring away from their feeding and spawning grounds. As far as our records go, the last seem to have been relatively very abundant in 1931, compared with 1932 and 1933. We have 29 references to their presence during fishing operations and they can be classified as follows :—

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* See also Ann. Rep. Fish. Bd. Scot. for 1930 (1931), pp. 20–21, where squid and cuttle-fish are reported as infesting the usual grounds.

† See Introduction for reference to Hjort.

‡ Ann. Rep. Fish. Bd. Scot. for 1932 (1933), p. 18.

General Remarks.	Associated catches.	Av. catch.
" Few " or " several " dog-fish	0, $\frac{1}{8}$, 1, $1\frac{1}{4}$, $2\frac{3}{4}$, 15, 16, 17 and 30	$9{\cdot}2^{9}$
" Many " dog-fish	0, 0, 0, 0, $\frac{1}{8}$, 1, 1, 3, $12\frac{3}{4}$ and 51	$6{\cdot}9^{10}$
Dog-fish (no indication of quantity)	0, 0, 0, $\frac{1}{2}$, $\frac{1}{2}$, 1, 1, 2, 20 and 40	$6{\cdot}5^{10}$

Indices denote number of catches averaged.

Ten references to whales suggest that catches may be small when they are present. The average catch is $4{\cdot}0^{10}$ crans, and the catches range from 0·0 to 13·5 crans. There were four references in 1931 and six in 1932. Seals and porpoises are mentioned in conjunction with two of these catches.

There are two references to sharks, with catches of 8 crans and $\frac{1}{2}$ box.

SUMMARY.

1. An attempt is made to relate catches of herring to the local abundance of associated jelly-fish, squid, dog-fish, etc. The data are derived from fishermen's descriptions of conditions at the time of fishing.

2. The observations as a whole suggest an avoidance by the herring of large numbers of jelly-fish.

3. Detailed results suggest that the herring tend most to avoid large numbers of " small " jelly-fish and particularly " small *white* " jelly-fish. This relationship also seems to extend to a group of observations in which colour is given with no indication of size. In two categories, particularly noted as " large " and " stinging " jelly-fish, this negative association is absent.

4. There is some evidence of a negative association between herring and the presence of large numbers of squid, dog-fish and whales.

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TABLE VI.

RECORDS RELATING TO QUANTITIES OF JELLY-FISH, BUT WITH NO INDICATION OF SIZE, TYPE OR COLOUR.

Date.	Area.	Remarks on label.	Catch.	Av. catch at port for week.
14.7.31	Shields	Very few jelly-fish	12·0	15·2
12.7.31	,,	Few jelly-fish	70·0	16·4
9.6.33	Scot. E.	,, ,,	51·0	10·0
24.7.31	Shields	,, ,,	18·0	20·4
6.9.31	,,	,, ,,	4·0	10·2
30.7.31	,,	,, ,,	3·0	17·1
3.7.31	,,	,, ,,	1·5	17·5
18.7.31	Scot. E.	,, ,,	1·25	2·0
22.7.31	,,	,, ,,	1·0	2·8
7.7.31	,,	Some jelly-fish	17·0	10·2
8.7.31	,,	,, ,,	6·25	10·2
7.8.31	Scot. E.	Lot of jelly-fish	8·0	4·3
23.6.31	,,	Plenty of jelly-fish	40·0	19·6
17.6.31	,,	,, ,,	10·0	9·1
21.7.31	Shields	,, ,,	10·0	20·4
16.6.33	Scot. E.	,, ,,	2·0	7·9
25.6.31	,,	,, ,,	2·0	19·6
5.8.31	,,	,, ,,	0·0	4·3
4.8.31	,,	,, ,,	0·0	4·3
13.7.31	Shields	Jelly-fish plentiful	43·0	15·2
29.6.31	,,	,, ,,	14·0	17·5
3.7.31	,,	,, ,,	8·0	17·5
5.7.31	,,	,, ,,	5·5	17·5
17.7.31	,,	,, ,,	5·0	15·2
19.7.31	,,	,, ,,	4·5	15·2
30.6.31	,,	,, ,,	2·0	17·5
31.8.31	Shields	Large quantities of jelly-fish	30·0	10·2
12.7.31	,,	,, ,, ,,	27·0	16·4
9.7.31	,,	,, ,, ,,	20·0	16·4
26.7.31	,,	,, ,, ,,	18·0	20·4
23.7.31	,,	,, ,, ,,	16·0	20·4
28.7.31	,,	,, ,, ,,	11·0	17·1
22.7.31	,,	,, ,, ,,	11·0	20·4
8.9.31	,,	,, ,, ,,	4·0	12·6
29.7.31	,,	,, ,, ,,	3·0	17·1
15.6.33	,,	,, ,, ,,	0·0	2·8
7.9.31	,,	,, ,, ,,	0·0	12·6
6.7.31	Shields	Large numbers of jelly-fish	30·0	16·4
8.7.31	,,	,, ,, ,,	20·0	16·4
18.8.31	,,	,, ,, ,,	18·0	7·1
25.8.31	,,	,, ,, ,,	12·0	6·5
14.8.31	,,	,, ,, ,,	11·0	8·1
16.8.31	,,	,, ,, ,,	6·0	8·1
26.8.31	,,	,, ,, ,,	4·0	6·5
17.8.31	,,	,, ,, ,,	0·0	7·1
17.6.31	Scot. E.	Sea thick with jelly-fish	29·0	9·1
6.7.31	Shields	Jelly-fish very plentiful	18·0	16·4
2.7.31	,,	,, ,, ,,	5·5	17·5
28.6.31	Scot. E.	Sea alive with jelly-fish	3·5	16·0
14.7.31	,,	Jelly-fish here very bad	1·0	2·0

Note.—Scot. E. denotes the Scottish Eastern Fishery.

TABLE VII.

NOTES ON THE OCCURRENCE OF SQUID WITH HERRING CATCHES IN SCOTTISH WATERS, 1931.

Date.	Remarks on label.	Catch.	Av. catch at port for week.
17.6.31†	" . . . a chance inkfish."	29·0	9·1
17.7.31†	"A few squid and dogfish."	15·0	6·7
24.7.31	"A few squid and small jellies."	5·5	2·8
30.6.31	" . . . also a few squid."	3·25	15·2
27.7.31	"Squids, a few."	0·25	2·9
2.7.31	"Some squid."*	1·5	15·2
14.7.31	" . . . also some squids."*	1·0	2·0
22.7.31	"Some squid and a few jellies."	1·0	2·8
9.7.31	" . . . some squid."	0·5	10·2
15.7.31	" . . . many squid."	1·25	2·0
30.7.31	"Plenty squid."*	0·5	2·9
29.7.31	"Squid and dogs were plentiful."	0·125	2·9
28.7.31	"Squid very plentiful."	0·0	2·9
21.7.31	"Some dogs, squid."	2·75	2·8
23.7.31	"Squid and dogs."	2·0	2·8
17.7.31	"Squid."*	1·0	2·0

* Phæocystis present.

† Taken between Lats. 59°–60° N. The others are between Lats. 58°–59° N.

Notes on the Early Stages of two Polychaetes, *Nephthys hombergi* Lamarck and *Pectinaria koreni* Malmgren.

By
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Naturalist at the Plymouth Laboratory.

With 3 Figures in the Text.

PART I

NEPHTHYS HOMBERGI LAMARCK

TROCHOSPHERES of *Nephthys hombergi* Lamarck are readily obtainable at Plymouth when the adult worms are mature from June to September. The worms are dug out of the muddy sand on the lower regions of the shore, and their eggs and sperms obtained by slitting open the body cavity. Fertilizations are easily made in glass finger-bowls of clean sea-water. Although apparently ripe worms have been kept under sea-water circulation in the laboratory, and under a variety of conditions, none has ever been induced to spawn naturally. After some days the body walls of some individuals have split along the back and shed their genital products in that way; these, however, were probably unhealthy and abnormal. A high percentage of the eggs got by cutting open the worms have fertilized and given rise to cultures of strongly swimming larvæ. During the summers of 1932–34 much time and effort were expended in numerous attempts to rear these larvæ, but in no single instance was success obtained. It had been hoped to collect material for a detailed histological study of the development, for it may be of a straightforward and simple type that would throw light on various problems of Polychæte embryology. Although these hopes have not been realized it seems of value to describe the trochosphere of which no entirely satisfactory account exists, in spite of a few references to it by previous writers.

Claparède and Mecznikow (1868) seem to have been the first to have identified trochospheres and later larvæ from the plankton as those of Nephthys. They appear to have been guided in their identification mainly by the form of the bristles of their later stages, which closely resembled those of the adults of this genus. Fewkes (1885) following their identification described stages from what was apparently an allied species in the plankton at Newport, Rhode Island, U.S.A. He reared the larvæ from the trochosphere to a stage with about ten chætigers. He admitted that the identification was provisional until either the earliest stages were traced back to the parent, or the latest was reared into the adult. Häcker (1896 and 1898) and Leschke (1903) obtained from the plankton segmented larvæ which they referred to this genus, largely, so it seems, on the basis of the earlier papers. McIntosh (1908) followed suit with figures of three fairly late stages and gave an account of the history to date. Gravely (1909) also accepted the identifications of previous workers and described segmented Nephthys larvæ from the Port Erin plankton.

While it is likely that all these authors have quite correctly assigned their larvæ to the genus Nephthys—some of them have even been so bold as to name the species—final proof can only be obtained in the manner already indicated by Fewkes. A step in this direction was taken by Fuchs (1911) who, in the Plymouth Laboratory, made fertilizations of *Nephthys hombergi* collected from the same sandy bays as those from which my material has been derived. His larvæ, however, like mine, ceased to develop after about fourteen days, although they could be kept alive for a week or more longer. His did not feed although provided with cultures of diatoms and other algæ; mine, on the other hand, ate Nitzschia and Thalassiosira and probably other organisms as well. Fuchs' description and figures of his trochospheres were a big advance on anything done previously, but they lack certain interesting details and no indication of size is given. Only in broad outlines could they be said to agree with the Nephthys trochospheres of Claparède and Mecznikow and of Fewkes. The same remark applies when my drawings and description are compared.

Description of the Eggs and Trochospheres.

The eggs are spherical or almost so, finely granular and opaque; by reflected light the colour is pink. They are about 112 μ in diameter and are surrounded by a membrane 1·5–2 μ thick. After fertilization this membrane separates slightly from the egg and the polar bodies are then produced.

Twelve to sixteen hours after fertilization the larvæ begin to swim. In shape they are spherical with an apical tuft of long cilia at the anterior end and a prototrochal band of beating cilia round the equator. The cilia pass through the egg membrane that from now on forms the cuticle of the larva. The cells of the latter are crowded with oily-looking globules, and there is a certain amount of dark brown pigment scattered irregularly over the body. The larvæ are soon swimming forwards at a relatively rapid rate and rotating on their longitudinal axes.

After two or three days the long apical cilia disappear and their place is taken by shorter but more numerous cilia that cover a much larger area at the anterior end (see Fig. 1). The prototroch completely encircles the body a little behind the equator. It consists of three bands, the middle one being the broadest and carrying the longest cilia, while the anterior band is the narrowest and bears the shortest cilia. These three bands are all very close together. In front of the prototroch and situated rather ventrally there is on each side a small curved line of beating cilia, with what appears to be a slight depression immediately anterior to it. Posterior to the prototroch, but on the left side only, there is a curious long tuft (sensory ?) composed of several cilia loosely fused together. Of the very many larvæ examined only two specimens had such a tuft on the right side as well as on the left, and one of these larvæ showed structural abnormalities. The mouth is rather large and wide, and is strongly ciliated. The cilia of the upper lip reach as far forward as the prototroch. From the posterior border of the mouth a very broad neurotroch leads back towards the anus. Just before the latter is reached this neurotroch abruptly narrows to pass over a slight prominence that rises immediately in front of the terminal anus.

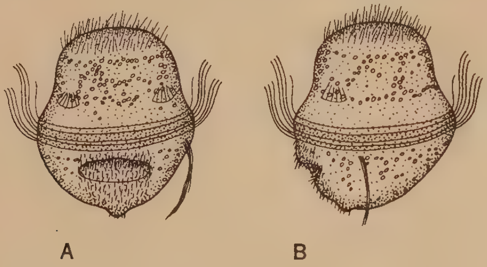

Fig. 1.—Drawings from life, × 156, of a four-days-old trochosphere of *Nephthys hombergi* Lamarck. A, ventral view; B, view of left side. Actual length, excluding apical cilia, approximately 167μ.

The trochosphere is not very transparent; it has a pale yellow tint. Dark brown pigment specks are scattered irregularly over both hemispheres and are especially numerous under the prototroch. Refringent greenish yellow globules of varying size form a sort of irregular broad band round the episphere; they are also present on the hyposphere where they sometimes form a band just behind the prototroch. These globules are close to the surface and often overlie the brown pigment specks. Globules of similar appearance occur deeper in the tissues, on the stomach wall, for example. The ectoderm is thick and apparently glandular. There are no bristles. The blastocoel is almost completely filled by the gut. The latter is well ciliated internally.

Despite the fact that the larvæ were feeding and lived in plunger jars for fourteen days or more, they scarcely developed further. The prototroch appeared to split up into five or six rows of cilia instead of the original three, and the episphere and hyposphere walls became a little thinner. No other changes were observed.

PART II

PECTINARIA KORENI MALMGREN

Very early larvæ of the Amphictenidæ have never been described, although late stages of Pectinaria, obtained from the plankton, have occasionally been illustrated and discussed (e.g. Gravely, 1909). This short note may therefore prove of some interest.

On 24th April, 1933, some specimens of *Pectinaria koreni* Malmgren were obtained when digging on the shore at Salcombe. When later, in the laboratory, they were removed from their tubes, they at once began to shed their genital products, a process that in the case of the females continued for several hours. Fertilizations were made, a good proportion of the eggs developing.

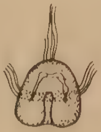

FIG. 2.—Gastrula of *Pectinaria koreni* about twenty-two hours after fertilization. Drawn from life, × 156. Actual length, excluding apical cilia, approximately 58μ.

The eggs were very small; approximately 62 μ in diameter. Each was closely invested in a transparent egg membrane that subsequently formed the cuticle of the larva. By reflected light the eggs were golden in colour, by transmitted light pale yellow; they were granular.

About sixteen hours after fertilization the embryos began to swim. They were almost perfectly spherical blastulæ with a tuft of long fine cilia at the apical end. A broad equatorial band of relatively long and very fine cilia formed the prototroch. The lower pole broadened and flattened, gastrulation taking place by invagination about twenty-two hours after fertilization. The gastrulæ (Fig. 2) swam rapidly forwards, rotating on their longitudinal axes. The limits of the blastocoel were irregular and not very distinct, but the archenteron was clearly defined.

Figure 3 shows several views of a three-days-old trochosphere. For a Polychæte it was an unusually minute, although beautiful, larva. It was characterized by large ventrally produced lateral lips which, with the anterior lip bearing the prototroch, overhung the mouth in the form of a hood. These large lips are very characteristic of the later stages of Pectinaria. This trochosphere was quite transparent and of a yellowish colour by transmitted light. A few dark brown oily globules were scattered irregularly over the episphere. Very few, if any, were present on the hyposphere. The ciliation was very complicated and difficult to follow; the drawings must therefore to some extent be regarded as provisional. The long apical tuft was, however, conspicuous and the prototroch, raised on a slight ridge, was continuous all round. The prototroch consisted of two bands of cilia, a narrow anterior one and a broad posterior, with a distinct non-ciliated gap between. The lips were edged with long cilia, some of them apparently sensory. At the lower posterior corner of the mouth a tuft of long cilia was visible in lateral view (Fig. 3, B). From there a narrow neurotroch ran towards the anus. Just in front of the latter a tuft of curious curled, and nearly motionless, cilia probably belonged to the future functional telotroch. The gut was divided into œsophagus, stomach and intestine, all well ciliated internally. The mouth could be closed. The larva swam relatively fast in the direction of the apical cilia, sometimes rotating on its longitudinal axis, although not so rapidly as before.

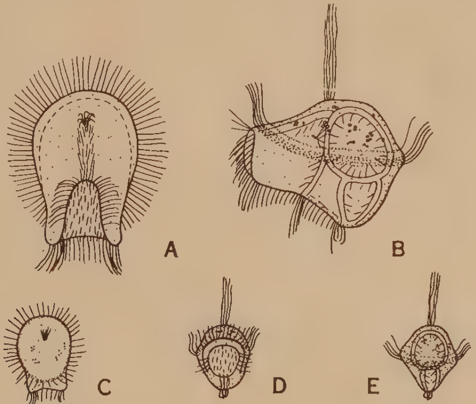

Fig. 3.—Sketches from life of a three-days-old trochosphere of *Pectinaria koreni* Malmgren. Actual length (apical plate to anus, excluding cilia) approximately 58μ. A, view from below, ×312; B, view of left side, ×312; C, view from above apical plate, ×156; D, morphologically ventral view, ×156; E, morphologically dorsal view, ×156.

All attempts to rear these trochospheres failed. They were seen to have a few minute specks of food in their stomachs, but it seemed that diatoms were too large for them. They lived for a few days and then died.

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The Ovary as an Indicator of the Spawning Period in Fishes.

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With 1 Figure in the Text.

Accounts of the ovarian development of the eggs of fishes have been given by Kisselevitch (1923), Mayenne (1927), and recently by Hickling (1930) and Raitt (1933). They have concluded that in the ovary of the adult fish there is a general egg-stock of small eggs, yolkless and transparent in fresh material, and with deeply staining cytoplasm in fixed and stained material. From this egg-stock a quota is withdrawn each year to be matured and finally spawned, and to this egg-stock a fresh batch is added each year by the development of oocytes present beneath the surface of the ovigerous lamellæ, the minimum period of development being two seasons.

It has occurred to us that measurements of the diameters of eggs, in ovaries well advanced towards spawning, may give evidence of the duration of spawning in a fish of which the spawning habits are unknown. For where the spawning period is short and definite, the batch of transparent yolkless small eggs, destined to mature and be spawned, will be withdrawn from the general egg-stock in a single group, sharply distinguishable, at least in the later stages of maturation, from the stock of small eggs from which it was derived. But when the spawning period is long and indefinite, the withdrawal of eggs from the egg-stock, to undergo maturation, will be a continuous process, and there will be no sharp separation between the general egg-stock and the maturing eggs. These will pass continuously one into the other. We have tested this hypothesis with four species of fish of known spawning habits.

MATERIAL.

We have compared the ovaries of Herring from the southern North Sea and Pilchard; Haddock from North Shields and Hake, and have also examined the ovaries of *Lepadogaster gouani*, the Cornish Sucker, a small fish of the tidal zone. We would acknowledge our thanks to Dr. E. J. Allen, F.R.S., for sending the Lepadogaster material from Plymouth, and to Mr. T. S. Leach, District Inspector of Fisheries at North Shields, for the haddock material. The ovaries were in all cases fixed in Bouin's Fluid, cut into sections and stained with iron hæmotoxylin and eosin. We would thank Mr. B. G. Clarke, Chief Laboratory Assistant at the Lowestoft Laboratory, for his care and skill in the preparation of the sections.

From 5 to 10 ovaries of each species, in the penultimate stages of ripeness, were examined, and the contained eggs measured. To make sure that the eggs measured had been cut approximately at their maximum diameter, only eggs in which the nucleus was visible were measured. The samples of eggs measured were unselected, except in the haddock, where the small transparent yolkless eggs were so numerous that towards the end of the measurements the smallest of these were omitted.

The results of these measurements are given in Table I as a frequency at each micrometer division, and a scale is added by which micrometer divisions can be converted into millimetres. They are also shown graphically in Figure 1, except that, for ease in producing the graphs, the eggs of the transparent yolkless egg-stock less than 6 micrometer divisions (0·095 mm.) in diameter have been omitted and the frequencies have been grouped in pairs.

RESULTS.

Comparing the measurements of the eggs in the ovary of the hake with those in that of the haddock, it will be seen that in the hake there is no sharp separation between the ripening eggs and the small eggs of the general egg-stock, whereas in the haddock there is a sharp separation, the larger maturing eggs forming a separate group. Between the two Clupeoids, the pilchard and the herring, there is the same difference. In the herring the separation is very sharp, for the mature eggs of the herring are exceptionally large. The difference noted between the hake and the haddock, the pilchard and the herring, is shown even more clearly in individual specimens than in all specimens combined (as they have been combined in Table I and Figure 1).

DISCUSSION.

The hake has a long spawning period. Hickling (1930) has shown that, though the main spawning months of the hake are from April to July, ovaries in the ripe condition are found in every month of the year except December, and he has found female hake actually running with eggs in March, July, August, September and late October in the waters to the

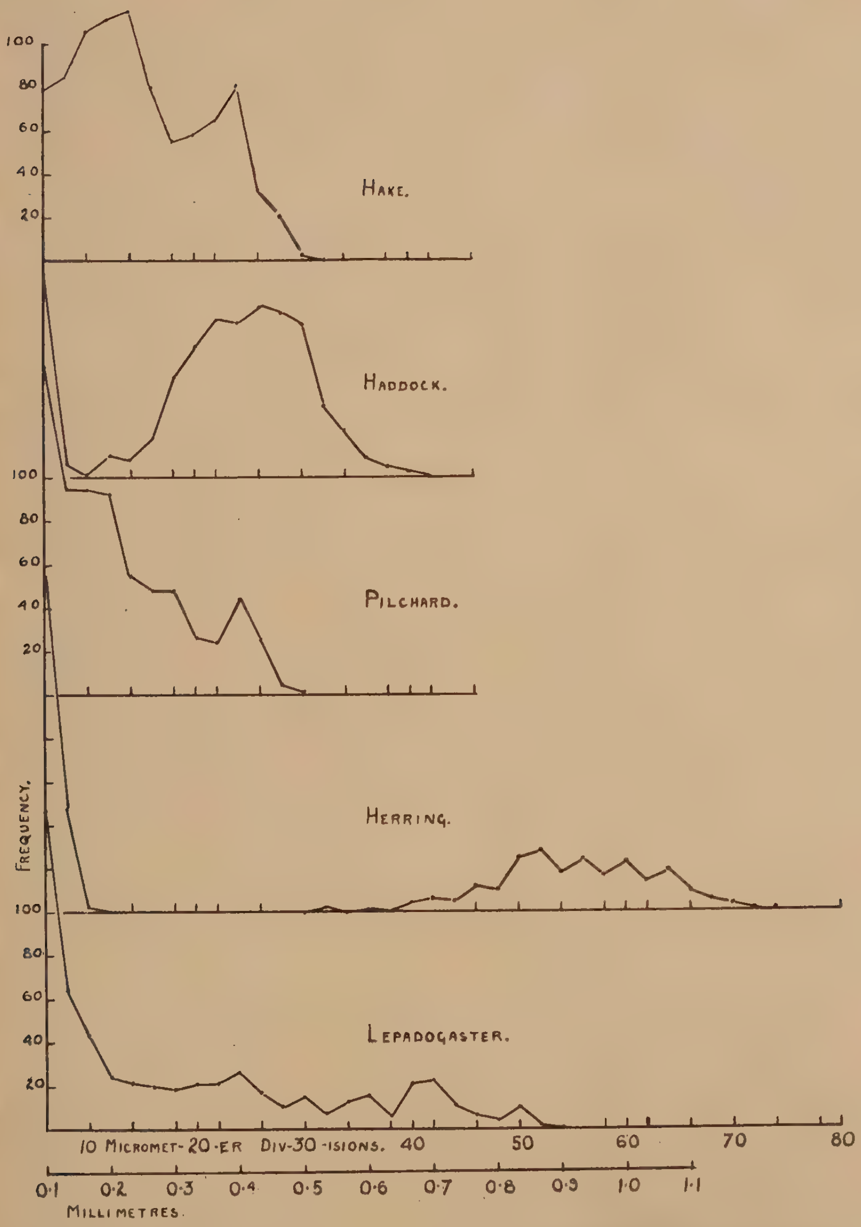

FIG. 1.—Frequency of diameters of the eggs in full ovaries of the five fishes given, grouped in pairs of micrometer divisions. (Date in Table I.)

south and west of Ireland. The haddock of the North Sea, on the other hand, has a more restricted spawning period. Damas (1910) shows that the eggs of the haddock in the North Sea are found from the end of January to the beginning of May, and that February, March and April are the principal spawning months.

The pilchard also has a long spawning period. Clark (1919) gives the spawning period in the neighbourhood of Plymouth as from April to October, with a maximum in July and August, and Russell (1929–30) confirms these findings with more recent material. On the other hand, the herring of the southern North Sea, according to Hodgson (1929) have a short and definite spawning period extending from December to February, and this is confirmed by the captures of herring eggs in the Straits of Dover.

In the case of the four species dealt with, the distribution of the frequencies of the diameters of the eggs in the ovary is in good agreement with the known duration of the spawning period, thus supporting the hypothesis set out in the introduction above. We intend to continue and extend this work with many other species of fish of which the spawning habits are known. If the measurements of the eggs in the ripe ovary correctly reflect the spawning habits, this may become a valuable method of deducing the spawning habits of new or rare species of fish.

Thompson (1915), Heidrich (1925), and Clark (1925) used this method of investigating the spawning habits of the halibut, sprat and grunion respectively. Clark, especially, shows an instructive series of graphs of egg-measurements, in which the fifteen-day spawning period of the grunion (*Leuristhes tenuis*) can be followed.

Kisselevich (1923) remarks with respect to Volga-Caspian herring (*Caspialosa caspia* and its subspecies) that their spawning is broken into three separate periods, spaced one to one and a half weeks apart. In the course of these intervals the next portion of eggs is ripening. The spawning is divided by intervals of time accompanied by change of location. Despite the relatively small size of the body and large eggs the Volga herrings are some of the most fertile fishes.

Ambroz (1931), having made a study of the Pacific herring (*Cl. har. pallasi* C. & V.), writes that the ripening of eggs also depends on the age of the fish : the older the fish the more similar they are with respect to condition of their ovaries. Their ripening is accomplished earlier, and their spawning period is shorter than that of younger herrings.

As far as we know, however, the method has not been used in comparing one species with another. The graph of the measurements of the eggs of *Lepadogaster gouani* drawn in the figure very much resembles that of *Leuristhes tenuis*, and suggests that Lepadogaster also may spawn at frequent intervals over a prolonged period of time. Precise information as to the duration of spawning in this species seems to be lacking however.

Another point that occurs to us is that attempts to use Hjort's scale of maturity-stages encounter difficulties when applied to a fish with a prolonged spawning period. For as the eggs contained in the ovary are progressively ripened and shed, the ovary itself grows smaller, and, to the naked eye, seems to reverse the stages by which it attained its full maturity. In such cases some other method of recording the stages should be used.

SUMMARY.

Measurements of diameters of the eggs in the ripening ovaries of four species of fish, namely the hake and haddock, pilchard and herring, give frequency-distributions which are consonant with the known duration of the spawning period. It is suggested that this method may provide information as to the spawning habits of new or rare species of fish.

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TABLE I.

Frequency of Diameters of Eggs at each Micrometer Division.

Micro. div.	mm.	Hake.	Haddock.	Pilchard.	Herring.	Lepadogaster.
1		74	510+	68		74
2		174	215+	143	7	210
3		248	300+	241	36	180
4		189	240+	232	61	149
5	0·082	90	190	187	114	127
6		47	70	90	106	92
7		32	24	62	49	53
8		38	6	52	37	40
9		47	1	43	11	24
10	0·166	50		51	2	27
11		56	1	44		16
12		55	3	53		17
13		56	7	40		7
14		57	3	25		9
15		58	6	30		12
16		46	4	26		14
17		34	15	22		6
18		29	23	23		11
19		26	24	25		8
20	0·333	37	30	16		9
21		21	31	11		12
22		29	28	10		5
23		36	45	14		16
24		38	36	19		17
25		43	36	25		9
26		19	44	17		13
27		14	35	8		4
28		5	44	2		7
29		6	32	2		3
30	0·500		45	1		10
31		2	26			5
32			22			5
33			11		2	2
34			15			2
35			7			11
36			6		1	13
37			3			3
38			1			3
39			4			3
40	0·669		3		1	8
41					3	13
42					2	12
43					4	10
44					1	4
45					4	7
46					4	3
47					8	3
48					6	1
49					4	3
50					15	7
51					10	3
52					15	1
53					13	
54					10	
55					8	
56					11	
57					13	
58					11	
59					6	
60					15	
61					8	
62					6	
63					8	
64					6	
65					13	
66					6	
67 and over					14	

Heterozygotes in a Wild Population of *Gammarus chevreuxi* Sexton.

By

E. W. Sexton and A. R. Clark.

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During the progress of the work on *Gammarus chevreuxi* it became increasingly evident that heterozygosity must exist in the wild population.

In the hope of solving the problem, a large collection was made in 1931, the "M. Expt." (**4**, p. 381), but an outbreak of bacterial infection in the bowls rendered the experiment a failure.

In 1933 it was decided to take another dredging and to work from as large a collection as possible in order to settle the question once for all.

This is the experiment described below.

THE 1933 D. EXPERIMENT.

The animals were divided into two lots, half being kept in as near natural conditions as possible, half in the incubator.

The air temperature in the incubator was kept at 21° C., and the water in the bowls registered a half a degree lower.

For the "natural conditions" a large outside shed was prepared, facing east, but shaded so that no direct sunlight entered. Daily readings were taken with Negretti and Zambra's standardised maximum and minimum thermometers of the temperature of the air and of the water in the bowls. The temperature ranged from 25·8° C. to —1·5° below freezing-point.

Summaries given in the following Table show the highest and lowest of the daily readings for air and water respectively and the average for the month of the maximum and minimum temperatures. The readings were taken at approximately the same time daily (10 a.m.) from February 20, 1933, to January 31, 1934.

TABLE I.

Date of Record.	Maximum temperature °C.		Date of record.	Minimum temperature °C.		Month and no. of readings.	Monthly average temperature °C.	
1933.	Water.	Air.		Water.	Air.		Water.	Air.
Feb. 22	6·5		Feb. 20	1·5	1·5	Feb. (4)	4·87	5·62
26, 28		7·0						
March 29, 30	12·0		March 1	6·0		March (30)	8·3	8·74
30		13·75	1, 21		6·0			
April 12	14·25		April 20, 22, 23	7·75		April (30)	10·25	10·35
14		15·75	20		6·25			
May 25	18·3		May 9, 10	10·75		May (28)	13·09	13·06
20		20·0	1		9·5			
June 8	22·5		June 22, 23	14·0		June (30)	16·45	16·6
9		24·5	22		12·75			
July 5	22·25		July 3	15·5		July (29)	17·98	18·26
27		24·5	1		14·1			
Aug. 7	23·8	25·8	Aug. 22, 23, 24	16·0		Aug. (25)	18·42	18·47
			22, 24		15·0			
Sept. 8	21·9		Sept. 28	9·0	7·5	Sept. (26)	16·6	16·57
4		23·0						
Oct. 1, 3	17·6		Oct. 30	7·25	6·0	Oct. (24)	12·8	12·74
3		19·0						
Nov. 3	11·4		Nov. 28	5·0		Nov. (29)	7·86	7·69
2		11·1	26, 27		4·0			
Dec. 2	8·0	8·0	Dec. 14	0·0	−1·5	Dec. (24)	3·16	3·01
1934.			1934.			1934.		
Jan. 19	9·6	10·25	Jan. 1	3·7	2·75	Jan. (24)	6·04	6·19

The time of the experiment coincided with a period of depression in the numbers of the population in the ditches. Owing to this unexpected difficulty sufficiently large numbers could not be obtained at one collection, and the dredgings had therefore to be carried on from February 20 to March 13, 1933.

Each dredging, as it was brought in, was examined, the mated pairs picked out, and half of them set out in the Incubator, and half in the "natural conditions." The preponderance of males in the catches, as will be seen in the following notes, may probably be accounted for by the floods in the Meadow preventing the nets working on the bottom of the ditches where the females and young usually live.

Feb. 20 : About 50 brought in ; 15 pairs taken out for the experiment ; the remainder being males and a few immature :

Feb. 24 : The ditches were frozen over, and the ice had to be broken to allow of dredging; 79 animals captured, 24 pairs taken out; the rest consisting of 30 males and 1 immature:

March 3: The ditches were full of water, and only the Gammarus swimming could be caught with the nets; 191 adults were taken—168 males and 23 females; 22 pairs were set out:

March 7: The Meadow and ditches were flooded like a pond, and even the bridge was knee-deep under water. The whole catch for a day's work numbered only 40, 37 males and 3 females; 3 pairs set out:

March 10: The water had subsided sufficiently far to permit of dredging in the ditches, but the Gammarus were found higher up the Meadow than usual, in the shallower water. 117 were caught, 67 males, 47 females, and 3 immature; 28 pairs were set out:

March 13: 130 were brought in, 69 males and 61 females; 60 pairs were set out:

The experiment now numbered 76 pairs in each division.

Two later dredgings were made, one on April 20, when the total catch was 18, 5 males and 13 females; and one on May 9, of 34 animals, 19 males, 11 females, 1 immature and 3 young just extruded. Ten pairs from the latter haul were later included in the "natural conditions" division.

The numbers of the young hatched in the F_1 and F_2 generations, and the variations are tabulated below, followed by details of the more important mutating stocks in the "Natural Conditions" part of the experiment.

NATURAL CONDITIONS.

It will be seen from the following Table that, in the Natural Conditions part of the experiment, the mutations or variations fall into definite groups, and that, apart from those changes in the coloured and the white pigments which have occurred in all our cultures, new groups have appeared, such as "Melanin-lag," or delay in the deposition of the black pigment; "Dwarfing," or delay in the body development; and "Gradual Normal" or increase in the white pigment. The two first of these can be directly traced to the effect of low temperature on the organism.

I. *Delay in black pigment deposition*—Melanin-lag. In Stocks *D. VII*; *VIII*; *IX*; *XIII*; *XVI*; *XX*; *XXIV*; *XXV*; *XXIX*; *XXXII*; *XXXIII*; *XXXVI*; *XXXVIII*; and *XLIX A*; and also in *XLIV* (*2*) and *LXX*.

From time to time in our work we have noted specimens showing a reduction in the amount of the melanic pigment deposited in the eye before birth. Sometimes we have been able to correlate this with a

FROM OUTSIDE MATING OF ♀.

Stock No.	F_1 Black.	F_1 Spotted.		F_2 Black.	
D. II A.	6	1	All reddish→B.	—	
D. III A.	19	3		417	40 with very thin retic.
D. IV A.	No eggs			—	
D. V A.	No eggs, ♀ very small.			—	
D. VI A.	No eggs			—	
D. VII A.	All eggs thrown off except 1			—	
D. VIII A.	8	6	2 spd. very reddish (1 irreg.) →B.	—	
IX A.	10	5	1 irreg.	—	
D. X A.	36		8 and 1 HN. spd. Dwarfing	439	1 HN. spd., 2 No-antenna regenerated to normal
D. XI A.	28	11		256	B., 29 BN., 1 HN. **Nowhite recessive** F_2, 1 very irreg.
D. XII A.	Eggs thrown off			—	
D. XIII A.	18			27	F_3, 25 B.
D. XIV A.	No eggs ; ♀ very small			—	
D. XV A.	,,			—	
D. XVI A.	,,			—	
D. XVII A.	,,			—	
D. XVIII A.	,,			—	
D. XIX A.	,,		♀ very small	—	
D. XX A.	3 (♀ very small) 1 survivor, ♀×♂ from *XX* gave			26	B., 3 BN., 1 HN. *Increase* of white pigment.
D. XXI A.	Eggs thrown off			—	
D. XXII A.	Eggs thrown off			—	
D. XXIII A.	23	4	1 irreg.	286	100 with deficiency of white pigment.
D. XXIV A.	11	2	Parent ♀ very small	—	
D. XXV A.	No eggs ; ♀ very small			—	
D. XXVI A.	,,		,,	—	
D. XXVII A.	,,		♀ Clotted-eyes	—	
D. XXVIII A.	,,		♀ very small	—	
D. XXIX A.	,,		,,	—	
D. XXX A.	,,		,, another generation	—	
D. XXXI A.	15	1	1 reddish→B., gave B. offspring	385	B., **26 Red. Red-eye recessive** (r_2). Melanin-lag and *Increase* in white.
D. XXXII A.	30	5		202	1 reddish in winter brood.
D. XXXIII A.	30	16	Survivors 3♂, 11♀	263	(54 spotted).
D. XXXIV A.	19	3	Some very reddish	16	
D. XXXV A.	20		Ten survivors, all ♀	—	
D. XXXVI A.	25	1		36	1 pair gave young alm. BN. (1 spd.)
D. XXXVII A.	1 spd.			—	
D. XXXVIII A.	27	4		279	B., 1 BN., 1 HN. *Gradual Normals.*

FROM INSIDE MATING OF ♀.

Stock No.	F_1 Black.		F_2 Black.
D. II	22		108 B., 1 HN.
(1) *D. III* ♂ & ♀	35		26
(2) *D. III* & *XXV* ♂	41		24
(3) *D. III* & *XII* ♂	40	2 ♀ white gonads→normal	232 B., 1 BN.
D. IV	70		22
D. V	27	2 Dwarf	151 B., 3 BN., 1 HN. *Nowhite*, not proved.
D. VI	10	♀ VI put with ♂ *LIII*	—
D. VII	59		168 B., 2 HN. Melanin-lag in 2 winter broods.
(1) *D VIII* ♂ & ♀	58		361 B. **18 Red. Red-eye recessive** in F_2, new. Melanin-lag in 1 brood.
(2) *D. VIII* & *IV* ♂	42		56
D. IX	65	2 Dwarf	354 B., 8 BN., 7 HN. and 10 alm. N. *Nowhite* not proved, Pigment-lag.
D. X	117		189 B., 2 **DR.**, 4 Reddish **Lilac N. Red-eye Recessive** new. Allied to Lilac. *Nowhite* variation.
D. XI	51		32
D. XII	57		234 B., 1 BN., 1 HN. (and 2 irreg. and malformed).
D. XIII	89		410 B., 17 BN., 1 HN. **Genotypic Nowhite** in F_2.
D. XIV	84	3 Dwarf	161
D. XV	71		209 1 irreg.
D. XVI	81 B., 3 BN., 4 alm. N. *Phenotypic Nowhite*		617 B., 13 BN., 2 HN. *Phenotypic Nowhite.* Melanin-lag.
D. XVII	60		87 *Increase* of white pigment.
D. XVIII	79		229 B., 2 BN., 7 **Red. Red-eye recessive**, not proved. *Nowhite.*
D. XIX	92		242 B., 1 HN.
D. XX	53 and 2 irreg. and malformed → almost normal		354 B., 2 BN. (and 1 alm. BN.). *Nowhite*, not proved. Melanin-lag.
D. XXI	40		44
D. XXII	36	In 1 brood, 3♀ out of 8, white gonads	117 17 alm. BN.→normal. *Increase* of white.
D. XXIII	99		232 22 with deficiency of white.
D. XXIV	35		421 B. and 3 irreg. Melanin-lag in 21.
D. XXV	50		107 B., 1 BN. Melanin-lag.
D. XXVI	45	*Gradual Nowhite*	102 B., 35 BN. and 2 alm. BN., **Genotypic Nowhite.**
D. XXVII	54	18 survivors, all females	—
D. XXVIII	83		253
D. XXIX	72 and 1 malformed, 2 normals→ malformed		549 B. and **7 Red. Red-eye** not proved. Irregularity and Melanin-lag in 1 winter brood.
D. XXX	60		263 *Increase* in white pigment.
D. XXXI	69 and 9 Irreg. Irregularity		1054 B., 5 BN., 6 HN. spd. **Red-eye recessive** (r_2).
D. XXXII	65		211 Melanin-lag and *increase* of white
D. XXXIII	96	17 of these→BN. and 1 alm. N.	589 Excess of ♀ 39 to 13 ♂. *Gradual Nowhite*; Melanin-lag.
D. XXXIV	91	About 30, reduction of white pigment	84 (3 almost BN.).
D. XXXV	91		34
D. XXXVI	58		216 Melanin-lag in 2 broods.
D. XXXVII	49		159 and 1 HN.
♂ (1) *D. XXXVIII* ♀	21	Surv. 1 ♂, 8 ♀. Excess of ♀. Crossed with *XXXVIII A.* gave	8 5 B., 6 BN., 1 HN. and 1 alm. N. *Gradual Normal.*

OUTSIDE MATING.

	F_1			F_2	
Stock No.	Black.	Spotted.		Black.	
D. XXXIX A.	15		Survivors 2 ♀×♂ from *XXXIX* gave	75	
D. XL A.	Eggs disintegrated in pouch			—	
D. XLI A.	No eggs			—	
D. XLII A.	No eggs ; ♀ very small			—	
D. XLIII A.	,,			—	
D. XLIV A.	Eggs thrown off			—	
D. XLV A.	Infertile ♀, not Intersex, 7 matings with 3 males ; no eggs.				
D. XLVI A.	13	3	Three survivors, all ♀.	—	
D. XLVII A.	17	7	Two survivors, ♂	—	
D. XLVIII A.	22	6		95	
D. XLIX A.	22	3		203	B., 4 BN. and 10 alm. N.→ B. normal. *Increase* in white. Melanin-lag.
D. L A.	2		One survivor, ♂	—	
D. LI A.	24	3	One survivor ♂×♀ from *LIV A.*	27	B., 2 BN. *Nowhite,* not proved.
D. LII A.	8	3		19	
D. LIII A.	9 B. (2 spd.), **2 Red** (1 spd.) **Red-eye recessive** (r_2)			28	B. **5 Red.** 2 Dwarfs.
D. LIV A.	37			67	
D. LV	13			16	
D. LVI	9			3	
D. LVII A.	2	1	Survivors 2 ♂	—	
D. LVIII A.	20	1		13	
D. LIX A.	10	1		2	
D. LX A.	21			14	
D. LXI A.	1 spd.			—	
D. LXII A.	15	3		—	
D. LXIII A.	10	1		17	
D. LXIV A.	29	2		145	B., **3 Red. Red-eye recessive** (r_2).
D. LXV A.	6	2		—	
D. LXVI A.	15	1		1	
D. LXVII A.	23			6	
D. LXVIII A.	10	3		4	
D. LXIX A.	2	1	Survivors, 2 ♀	—	
D. LXX A.	27	1	♂×♀ of *LXX* stock gave	30	
D. LXXI A.	7			—	
D. LXXII A.	No eggs			—	
D. LXXIII A.	,,			—	
D. LXXIV A.	,,			—	
D. LXXV A.	3		Survivors, males		
D. LXXVIII A.	4	1	Survivor 1 ♀	—	
D. LXXIX A.	15	2		24	
D. LXXX A.	19	1		13	
D. LXXXI A.	24	2		2	
D. LXXXII A.	25			7	
D. LXXXIV A.	18			31	
D. LXXXV A.	33			7	
D. LXXXVII	21	1		34	B. and 2 HN. *Nowhite* not proved. In F_3 1 HN., white gonads.

INSIDE MATING.

Stock No.	F_1 Black.		F_2 Black.	
♂ (2) *D. XXXVIII* ♀	39	Surv. 2♂, 13♀. Crossed with *XXXVIII A.*	105	B., 1 HN. spd. and 4 alm. BN.
D. XXXIX	71	" White body " variation	62	B., 1 BN., 2 HN. " White body." *Nowhite*, not proved.
D. XL	100		48	
D. XLI	46		257	
D. XLII	65	Surv. 12 ♂, 7 ♀. 1 ♀ white gonads	45	2 ♂ and 1 ♀ "white body," 1 ♀ pale eggs.
D. XLIII	55	(19 spd.) excess of ♀, 41♀ to 8 ♂	286	(46 spd.) and 2 Irregulars.
D. XLIV	98		172	3 premature DR.→B.
—	—			
(♂ 1) *D. XLVI* ♀	29		175	B. and **18 Red. Red-eye recessive** (r_2). Reduction of white.
(♂ 2) *D. XLVI* ♀	19			
D. XLVII	49		262	(6 almost BN.)
D. XLVIII × LXX ♂	10		41	(1 alm. BN.).
D. XLIX	50		258	B., 1 BN. spd., 2 HN spd.
D. L	70		186	B., 1 HN.
D. LI	55		123	B., 4 BN., 2 HN. *Nowhite*, not proved.
D. LII	29		14	
D. LIII	62		253	B., 1 BN., **23 Red, 5 RN. Red-eye recessive** (r_2) and *Nowhite.*
(2) *D. LIII* × ♂ *LXX*	37		22	B., **2 Red.**
(3) *D. LIII* × ♂ *LXI*	34		13	B., 1 HN., **3 Red** (3 B. very thin ret.)
D. LIV	71		105	
D. LV	48		131	B., 3 BN. *Phenotypic Nowhite* in F_2.
D. LVI	58		55	B. and 1 BN. malformed and much spotted.
D. LVII	16		190	
D. LVIII	47		170	
D. LIX	74		209	
D. LX	93		189	
D. LXI	62		64	B., 8 BN., 5 HN. *Nowhite*, not proved.
D. LXII	60		19	
D. LXIII	49	*Gradual Nowhite ?*	74	B., 3 BN. (and 2 alm. BN.).
D. LXIV	89	1→HN.	323	B., **20 Red. Red-eye recessive** (r_2).
D. LXV	53		114	B., 6 BN. and 65 almost BN.→B. normal. *Increase* of white.
D. LXVI	51	Excess of females, 10 to 1 ♂	11	
D. LXVII	56		41	1 sl. irreg. and much spotted.
D. LXVIII	30	B., 5 BN. Survivors, 6♂, 14 ♀	199	B., 13 BN., 17 alm. BN. *Phenotypic Nowhite.*
D. LXIX	63	Survivors, 9 ♂, 16 ♀	40	
D. LXX	58		60	Premature extrusion, 1 DR.
D. LXXI	40		92	
D. LXXII	87		28	
D. LXXIII	66	Excess of males, 15 to 6 ♀	25	
D. LXXIV	61	Only 5 survivors, 4 ♂, 1 ♀	—	
D. LXXV	74	Excess of females, 10 to 3 ♂	26	
D. LXXVIII	19	Survivors, 1 ♂, 6 ♀	8	
D. LXXIX	10		19	
D. LXXX	40		12	
D. LXXXI	35		7	
D. LXXXII	43		3	
D. LXXXIV	102	Excess of males, 17 to 4 ♀	34	
D. LXXXV	81		86	
D. LXXXVII	17	Survivors, 1 ♂, 5 ♀	5	

sudden rise in the temperature accelerating the last stages of embryonic development, by which hatching may be so hastened that the young animal is born with the eyes Reddish Black, or even Dark Red, instead of the normal jet-Black, and a few days may elapse before they darken to the right intensity.

For many years the effect of high temperatures on the growing organism has been studied, particularly in relation to the eye-pigments, but until this experiment was started nothing had ever been observed as to the effect of extreme cold. It was of course known that by lowering the temperature, the embryonic development could be retarded to a great extent but it was now found that continued extreme cold during the incubatory period could and did in some cases so delay the deposition of the black pigment as to inhibit its action completely until after the young had left the brood pouch, the eyes at birth being a bright clear red colour with no trace of the dark pigment.

D. VII.

In this stock the first brood was hatched in mid-winter, on December 2, 1933, and extruded from the pouch on December 4, 5 very small young =1 Black, 1 Reddish Black, and 3 bright Red. On the following day, two had commenced to darken, and by December 29, before the first moult, all five were jet-black, and remained so. Eggs were laid on December 4, but did not hatch ; two later broods were all Black at birth.

In another brood of 7, from the same Stock, 5 hatched before the others, viz., 2 very Reddish Blacks, and 3 bright Reds. Four days later, all had become jet-Black and the 2 remaining in the pouch were extruded, both black-eyed.

D. VIII.

A brood of 19, extruded on February 12, 1934, from eggs laid during a period of intense cold, at the end of December, consisted of 8 Black, 8 Reddish Black, and 3 Dark Red. The dark pigment took several weeks to develop, but all eventually became quite Black, and gave normal Black-eyed offspring.

D. IX.

The delay in the deposition of the pigments, retinular as well as interommatidial, was very noticeable in this stock. In one brood of 22 (8 spotted and 1 HN.) (*D. 2185*) all were hatched with more red than black showing in their eyes ; many of them were a clear deep Red colour. All became Black before maturity ; and gave Black offspring. In another brood of 9 almost Nowhite, 4 were hatched Dark Red→Black normal-eyed and gave Black offspring.

A third brood of 15 consisted of 4 Black, 5 BN., and 6 Dark Red; all died immature.

In a fourth brood, 2 were hatched, one a very Reddish Black, and one dark clear Red. Both darkened, and became quite Black in a few days.

In another brood of 18 (extruded on the same day as the first brood of 22), 1 had the right eye normal Black, and the left, bright Red and irregular, with a large spot on the same side (Cf. *D. XXXIII*, p. 328; and p. 356). It died before reaching maturity.

D. XIII.

One midwinter brood, hatched January 10, consisted of 3 very small Black, 1 spotted and 2 very reddish→Black.

D. XVI.

In one brood hatched on December 12, 1933, with the temperature below zero, 12 young were noted, as very small and humped up, with bright Red eyes. By December 29, and before the first moult had taken place, the eyes were all jet-Black (2 animals almost BN., with the white pigment failing).

D. XX.

One brood of 3, consisting of 2 Black and 1 dark clear Red. The Red darkened rapidly and in two days became quite Black.

D. XXIV.

One midwinter brood, hatched on November 25–26, consisted of 20 " Red ": examined again on November 27 the eyes had darkened and became Black.

D. XXV.

In one midwinter brood of 12, 3 were born with bright Red eyes. Before maturity was reached the eyes had become jet-Black. The one survivor, a ♀, was mated with 2 Black males of the same brood, with no results.

D. XXIX.

In one midwinter brood, December 2, 1933, 3 out of a brood of 6 were Dark Red on hatching, but were quite Black ten days later.

D. XXXII.

One winter brood of 3 contained 1 Black normal and 2 Dark Red on hatching. These became Black in ten days, but did not survive to mate.

D. XXXIII.

Out of 26 pairs, one pair in 2 winter broods gave some bright Red-eyed young with the Black. The first, extruded with the temperature below zero, consisted of 24 Black (2 spd.) and 10 Red (1 spd.). The Reds were a bright clear colour which darkened gradually to RB., and then to Black.

In the second brood, examined within a day or two of extrusion, 9 were Black, 2 Dark Red, and 1 had a bright Red eye on the right side, and a normal Black left eye (cf. *D. IX*, p. 327). The two DR darkened; the Half-Red died.

D. XXXVI.

In 2 midwinter broods 1 very reddish was extruded on January 11, and 1 very reddish in a brood of 4 B. on January 17. Within a week the eyes had darkened to Black.

D. XXXVIII. A.

One brood of 7 just extruded were all dark Red, but darkened within a day or two to Black.

D. XLIX. A.

One brood hatched in midwinter, December 12, 1933, consisted of 6 young, 3 Dark Red (1 spd.), and 3 bright Red; others were in the pouch, but died. For 2 days the eye-colour remained unchanged; then it gradually darkened until, 17 days later, all six were definitely Black. By January 11, 1934, all were dead.

Two other examples, *D. XLIV* (*2*) and *D. LXX*, in which some of the young were Dark Red on extrusion, are referable to a different cause—not so much to a delay in pigment deposition, as to a premature hatching before the development in the egg was completed. In both cases the females were being examined under the microscope. In *XLIV* (*2*) three out of nine eggs were seen to break and the young emerge. Two had no white pigment, and one hardly any. They were examined 4 days afterwards, with the six others which had hatched later, all were found to be jet-Black, and to have the full amount of white pigment reticulation.

In *D. LXX*, when examining the female, 1 young was hatched and extruded on the slide. It was a rusty Dark Red, which became jet-Black within a day or two.

II. *Dwarfing.*

Many instances of greatly retarded development or "dwarfing" occurred throughout the stock, both in the F_1 and F_2.

A few typical instances are quoted below:—

D. V.

In an F_1 brood of 5, hatched on May 18, there were 3 survivors on September 15, 1 ♂ fully mature, normal size, and 2 Dwarfs. These two did not reach maturity till October 11; they mated on October 22, but their first brood was not hatched till December 11. They were still exceedingly small, but the young produced though few in number were normal size. Three broods were given in six months, 14 B., and 3 BN.—of which four, 3 B. and 1 BN. survived, all normal size, but died without offspring.

D. VIII.

Out of an F_1 brood of 28 Black, 19 survived, 2 "dwarfs exceedingly small," were seen four months later when most of the others were mature. At 9 months of age, 1 had become a very small female, the other was marked as "not yet mature." Two months later, it died "size and condition unaltered."

D. IX.

An F_1 brood, eggs laid April 4, 1933, hatched April 26; 27 Black young. On September 3, there were 14 survivors, 5 of which were mature, 7 others normal size, nearly mature, and 2 exceedingly small, which were put in a separate pot for observation. Though of over four months age, they were no larger than young animals three weeks old. By the end of September one had started to grow, and had attained normal size by October 23, a ♂; the ♀ was also sexually mature, but still exceedingly small, with 2 eggs in her pouch. These were thrown off; other broods were laid, of only 1 or 2 eggs, the female's pouch being too small to hold more. None hatched until February 15, 1934, when 1 normal sized spotted Black young was born (died immature). The female laid another batch of eggs, and was eaten by her mate. In the F_2 brood, *D. 2168*, in which melanin-lag occurred, there were 5 B. and 4 Dark Red; 1 of the 5 Black was a dwarf, and looked, when the others were mature, as if it had only just reached the first growth stage.

D. X. A.

The Outside brood was hatched on March 16, 1933, and consisted of 37 Black (9 spd. 1 HN.), of which 29 survived. Six months later, September 14, 3 of these were still so small as to look like the next generation. On October 16 they were still not mature: on November 1 they looked like young ♂ and ♀, but died without breeding.

D. XIV.

In one F_1 brood of 17 Black, hatched on May 26, 1933, and divided into two lots, seven in one bowl were mature and breeding by the beginning of October, i.e. mature at 4 months, whilst in the other at the same date 3 only were left, exceedingly small. One of these survived but at 8 months had made no appreciable growth, and died without attaining sexual maturity.

D. LIII. A.

In one F_2 brood of 11 Black, *D. 595*, August 17, 1933, 5 were found on November 18, 3 just mature, and 2 very small and now Half Nowhite. Three months later they were still marked as exceptionally small, with no appreciable growth. One—a very small female—survived to maturity, May 24, 1934, but died without mating.

III. *Gradual Normals.*

Gradual Nowhites, with the characteristic feature of steady and gradual reduction of the interommatidial white pigment, have been recorded in different stocks from 1917 onwards.

The effect of the reduction-factor was the gradual change from normality to nowhite; but another variation, the Gradual Normal, has been found in this experiment in which the reverse action obtains, a gradual change from nowhite to normality.

Some factor or factors modifying the rate of the formation and deposition of the white pigment are evidently present in this type. In some instances the extreme cold would seem to be the excitant cause of this appearance, the low temperature retarding the formation of the white in the later embryonic stages. The result is an eye nowhite at birth, the absence of the pigment being made good later by a rapid increase in the rate, bringing the amount deposited up to normal.

It is an interesting fact that these *reduction* and *increase* factors can exist in the same stock with the Nowhite factor inhibiting the appearance of any white pigment—see e.g. *D. XIII*, with genotypic Nowhite, and Gradual Normals in the same brood. Instances of the gradual increase of white making good the deficiency caused by the extreme cold, are *D. XXXII*, and *D. XLIX*.

D. XXXII. Increase in white pigment.

Black Nowhites were given by two pairs, the young hatching on the same day, March 12, 1934. One brood numbered 5 Black normal, 4 BN.; and the other 3 B., and 5 BN. In ten days, white pigment had been deposited to the usual amount, and two animals had even developed spots. Two reached maturity and gave Black young perfectly normal-eyed.

D. XLIX. A. Increase in white pigment.

Out of the 4 F_1 pairs of this stock, one pair only gave Nowhite in its offspring. The brood was a mid-winter one, 14 in number, consisting of 10 Black almost BN. (1 spd.), with only 1 or 2 flecks of white in the eyes, and 4 BN. (1 spd.). All developed the white reticulation and became perfectly normal-eyed, and gave 6 normal-eyed young. The other broods of the pair, 1 B.; 2 B.; 4 B. (2 spd.); and 22 B. (5 spd.) were all normal-eyed.

Instances which cannot be attributed to cold and of which the cause is not evident, will be found in *D. XXX.* (see also *D. IX.*), and *D. XXXVIII.*

D. XXX. Black Nowhites appeared in the F_2 from 1 pair only, out of 15 effective pairs. The brood hatched in midwinter consisted of 20 Black (4 spd.), all with very thin reticulation, and 3 BN. All became perfectly normal-eyed, the BN. showing the commencement of a very faint white reticulation 9 days after birth, and developing the full quantity of white pigment before maturity. Two of the BN.→normal mated and gave broods as follows: 7 Black norm.; 2 B. norm.; 19 B. norm. (2 spd.), and 1 thin retic.; and then a brood of 10 Black, 4 almost nowhite, and 3 BN. (1 spd.); and 2 B. norm. and 1 almost Nowhite.

All the members of the fourth brood→quite normal and developed the full amount of white pigment. The delay in the formation of the white pigment in this case could not be attributed to the effect of low temperature as the brood was hatched in August.

D. XXXVIII.

The ♀ *XXXVIII* produced a brood of 27 Black normals (4 spd.) in her mating with an Outside male, *XXXVIII A.* Sixteen survived, 6♂ and 10♀ and an F_2 of 281 B. was hatched.

The only appearance of anything out of the normal occurred in the third of 4 broods from Pair 2; the broods numbered 4 B.; 9 B.; 2 B. spd., 1 BN., 1 HN. spotted; and 29 Black (1 spd.) All died immature —so that the nowhite could not be tested, but they are probably the same as the Nowhites from the female's other matings.

The ♀'s brood from her "Inside" mating, *D XXXVIII (1)*, numbered 21 Black normals, 9 reaching maturity, 1 ♂ and 8 females.

One F_2 brood of 8 B. normal was hatched in the brood-bowl, the male and female died, and to the remaining seven females, a male from the ♀'s previous brood was added (*Pair*× *2*). This male unfortunately proved a cannibal, and after two more F_2 broods had been hatched (*D. 2271* and *D. 2426*), all the females and some of the young were eaten.

Brood D. 2271 consisted of 8 young, none of them with normal reticulation, and all but one spotted, viz., 2 BN. spotted both sides; 2 BN. spd. right side; 2 BN. spd. left side; 1 HN. right side, only a fleck or two on left side and spotted both sides; and 1 almost BN. unspotted. This brood had an interesting development; hatched on March 30, 1934, it was re-examined on April 19—7 left, none BN.; the 1 unspotted→normal; the HN. spd. still HN. on right side, but normal on the other; of the other 5, "BN. spd.," 4 had become normal one side, and 1 on both sides, while in some the spots had changed shape and position. Re-examined later, six were found, all had become perfectly normal, with white reticulation (except one still half nowhite left side), and the spots had again altered. One male and 4 females had become mature, and had given 23 Black young (1 spd.) all normal-eyed.

Brood 2426 numbered 5 Black normal, none survived.

The ♀ then mated with a third male, *D. XXXVIII (2)*, and had 3 broods, 39 Black. Fifteen survived, with again a great preponderance of females, 13 to 2 males. Intermatings of the 2 ♂♂ and 6 females produced 105 Black (4 spd.) and 1 HN. spotted→normal later. The 6 remaining females were put with a male from *XXXVIII A.* (the female's previous brood) (*Pair×3*) and gave an F_2 95 young, viz., 67 Black normal, 20 BN. (1 spd.), 1 HN., and 7 almost BN. (1 spd.). The first brood of these numbered 27, none normal (*D. 2272*), 20 BN. (1 spd.), 1 HN., 6 almost BN., hatched on March 30, 1934; examined three weeks later all had become perfectly normal-eyed, and in July when they were found breeding, 47 young were taken out, all with normal eyes (and 2 spotted).

It may be worth noting that these 3 stocks (with the same female parent) gave B. normals when mated *inter se*, 8 B. and 106 B. (1 HN.), but when crossed with the other stocks, a large number were born with greatly reduced or with no reticulation, e.g.:

XXXVIII (1)×A. gave 5 normals to 8 greatly reduced.

XXXVIII (2)×A. gave 67 normals to 28 greatly reduced.

D. LXV. Increase of white pigment.

Five out of seven F_1 pairs gave young showing great deficiency of white pigment at birth up to nowhite. 118 were normal-eyed; 45 had very little white reticulation; 17 were practically nowhite, with only 1 or 2 flecks of white; and 6 were completely Nowhite. All without exception developed the normal amount of white, one of the "BN." even becoming spotted. There was no F_3 generation.

This is the stock referred to in the last paragraph (**3**, p. 693), but by a clerical error the total was put at 254 instead of 186. It should read "an F_2 of 186 Black young was hatched, consisting of 118 normal-eyed. . . ."

IV. *Variations in the interommatidial pigment.*

The two definite types of Nowhite eye were represented in this experiment, Genotype and Phenotype; in addition also Gradual Nowhites and Gradual Normals occurred and, as will be seen in Tables II and III, numerous cases of BN. and HN. were recorded in many stocks appearing sporadically. Few of these could be tested owing to the high mortality amongst them.

Several stócks are described in detail below :—

D. IX.

This stock would appear to be one of those in which several modifying factors are present. Although only a few of the variant specimens survived to maturity yet they are sufficient for evidence of the *increase* of the white pigment after birth, and of the *Phenotypic* Nowhite variation, in which the animal affected, though it never develops the white itself, is yet able to transmit it to its offspring.

The F_2 consisted of 354 Black normal eyes, 8 BN., 7 HN. and 10 almost Nowhite.

Of the 8 BN. (7 from winter broods, 1 from a June brood) 6 died before they could be proved; one, spotted, developed white pigment on the left side, none on the right, i.e. Half Nowhite. It was mated with another HN., right side, and gave Black normal young. The eighth BN. reached maturity unchanged, a male, and was proved Phenotypic by a cross with a genotypic BN., from *Stock D. XIII.* The offspring consisted of 19 Black, all with the normal white reticulation, showing that the white was brought in by the phenotype, the genotypic nowhite possessing a factor inhibiting its appearance.

Of the 7 HN., 5 were nowhite on the right side, 2 on the left. All died without offspring except one, a female; she was mated with a phenotypic BN. from Stock *D. XVI*, and gave 22 Black normals (9 with thin reticulation).

Nine of the 10 almost Nowhite survived to maturity. In 8 of these the white pigment increased to the normal quantity in both eyes; in the ninth it developed in one eye only, the left.

D. XI A., probably *Genotypic Nowhite.*

A brood of 28 Black with marked instability of the white pigment. Eleven were spotted at birth, with rather unusual uniformity in the position of the spots, 6 being situated on the dorsum, and 5 on the right side of the head.

Twenty-one reached maturity, 14 males and 7 females, but of these only 15 were effective. Seven pairs were set out, and one female after giving 7 Black young with one male, was mated with a second male, and had 10 Black.

One pair only, Pair 2, unspotted, gave Nowhites. The offspring consisted of 65 Black (4 spotted), 28 Black Nowhites and 1 Half Nowhite (spotted on the same side as the Nowhite eye). The same female had one brood in the brood-bowl (probably with the same male) of 3 Black and 1 BN.

Another pair gave 1 with a very irregular left eye and spots on both sides, and 1 almost Nowhite out of 53 Black young, whilst a third pair had 4 almost Nowhite (2 of them with large spots both sides) amongst their 25 Black offspring.

All the other pairs hatched normals.

Four only of the BN. reached maturity, 3 males and 1 female, and of these 3 died without offspring. The remaining BN. male mated with a B. normal female of its own brood, and had 1 brood of 2 B. normal and 1 BN.

This, though not proved, is probably the *Genotypic Nowhite.*

D. XIII.

Genotypic Nowhites appeared in this stock in the F_2. They were proved by crossing with other known genotypic nowhites, with which all BN. offspring were given—and also with seven different phenotypic stocks, with which only Black normals were produced.

Seventeen F_1 pairs were effective, and out of these, three gave some Nowhites in their broods, as follows :—

Pair 8, 12 B., 1 BN. ; *Pair 11*, 9 B., 2 BN. ; *Pair 15*, 33 B., 11 BN. and 7 almost BN. at birth (→normal later) ; and 2 females, mating in the brood-bowls gave 6 B., 1 BN. and 4 B., 2 BN., respectively. All the other matings gave normal-eyed young.

A good example of the *Gradual Normals* appearing in the same family with the genotypic nowhites will be found in the *Pair 15* offspring, the 7 hatched "almost nowhite" had become fully normal a month later. In another family (*Pair 13*) 1 hatched almost Nowhite →HN.→ perfectly normal ; a second one, almost N.→HN. on the right side, perfectly normal on the left, gave all normal-eyed young.

D. XVI. Phenotypic Nowhites.

The Nowhites appeared in the F_1. Four broods were hatched, the first with all the young, 17, normal-eyed. The second numbered 33, one almost BN. ; one of the normals →BN. later and one →HN. in the right eye, left eye part nowhite. The third consisted of 19 B., 1 BN. and 3 partly BN., all with the reticulation thin and broken. One normal →BN. and one of the part-Nowhites →BN. female.

The latter female, and one of the normal eyed B. females had rows of "*white-eggs*" in the gonads (cf. Lilac, **4**, p. 394). Like the Lilac "white-egg" females the normal B. female gave no offspring, but the BN. female, though her gonads looked the same, laid eggs tinged with pale green colour, and evidently fertile, two small broods of 4 B. normals hatching out.

The dilution or absence of colour in the gonads and eggs appears now and again through this stock. For example, a sister female of the two just mentioned gave a brood of 3, one a BN. which had gonads and eggs of a bright emerald-green shade instead of the usual dark green verging on black.

The fourth F_1 brood consisted of 12 Black, one almost Nowhite and 2 BN.

A number of test matings were made, crossing the phenotypic nowhites of this stock with the genotypic Nowhites of *Stocks I*, *D. XIII* and *D. XXVI*; with phenotypic Nowhites of other stocks; and finally mating them together in the stock. In all the cases, only normal-eyed Black young were produced, all with the usual amount of white pigment, but it is a curious fact and not without significance that all the survivors without exception reached maturity with very little or none of the white pigment left, as if the deposition of the pigment must have been reduced or ceased soon after hatching.

One pair of the F_1 survivors of the *D. XVI* BN. matings gave a brood of 3 young, 1 Black and 2 BN.

D. XVIII. Phenotypic Nowhite.

The Nowhite occurred in one brood only, of 8 Black (1 spd.), 2 BN., from a back cross mating of the parent ♂ *XVIII* with an F_1 B. ♀.

The 2 BN. reached maturity, male and female, and mated. The female was eaten, and the male was then tested with two different genotypic Nowhite stocks, *D. XIII* and *D. XXVI*, and gave Black normal-eyed with both. The survivors, as recorded for similar matings in the previous Stock *XVI*, all suffered reduction and loss of the white pigment.

D. XX A. and *XX.*

Six pairs and 13 mixed matings were made amongst the F_1 survivors of the Inside mating of ♀ *XX*. Only one pair gave anything out of the ordinary, *Pair 1*, producing 2 BN. in a brood with 25 Black. The male was then mated with the only survivor of the Outside *XX* brood, a Black female—and had offspring, 25 Black normal, 3 BN. and 1 almost BN.→ perfectly normal (increase of white pigment) and 1 HN.

D. XXVI. Genotypic Nowhite.

The Nowhite of this stock differs from *D. XIII*, the other genotypic Nowhite which arose in the D Experiment, in that a *gradual* reduction of the white pigment ending in Nowhite (in appearance) took place in the F_1 generation, and the pure heritable Nowhites segregated out in the F_2. The gradual reduction is not exactly comparable with our "Gradual Nowhite" variation (**3**, p. 693).

Eleven F_1 survived, but only 3 pairs gave offspring—and one Back Cross of ♂ of *Pair 3* with the F_2 BN. ♀ from *Pair 1*. The results were as follows :—

Pair 1. Both parents had become practically BN. ; they gave 1 brood of 8 Black (1 spd.) and 1 BN. (→♀ and mated with ♂ *3*).

Pair 2. Parents with thin reticulation, had 55 Black (10 spd.), 2 almost Nowhite (1 spd.).

Pair 3. The male had become completely Nowhite, the female almost. Six broods were hatched, 41 Black (14 spd.) and 34 BN. (1 spd.).

The figures for the different broods are, 2 B. (spd.), 6 BN. ; 3 B. (2 spd.) ; 14 B. (4 spd.), 11 BN. (1 spd.) ; 3 B. (2 spd.), 10 BN. ; 16 B. (3 spd.), 6 BN. ; and 3 B. (1 spd.), 1 BN.

After six weeks 15 survivors of the B. normals were examined, 11 had remained normal, but 3 were now BN. and 1 almost BN. There were 15 survivors of the BN, which, mated later *inter se*, gave all BN. offspring.

The Back Cross referred to above of the BN. male *Pair 3* with the F_2 BN. female from *Pair 1*, was a mating between two types of Nowhite (phenotypic and genotypic). One brood was produced, 1 Black and 5 BN. One only survived, a BN. ♀, which was mated with the Genotypic Nowhite of Stock I and gave 20 BN. young. Many other crosses were made with the Nowhites of other types, giving as to be expected, Black normals with the phenotypic and Black Nowhites with the genotypic.

D. XXXIII is a typical example of the *Gradual Nowhite.*

Five broods were hatched in the F_1, all perfectly normal-eyed at birth, but all the survivors suffered the gradual reduction of the white pigment characteristic of this variation, ending in 17 cases as completely Nowhite and in 1 other case almost nowhite. Fifty-two animals reached maturity ; females were greatly in excess, 13 males to 39 females (cf. also *XXXI A*. 3 ♂, 11 ♀ survivors).

The offspring from their matings, 589 in number, were all born with normal-eyes, but these, as with their parents, steadily lost the white pigment. Out of the 33 survivors, only 16 remained fairly normal, 1 had very thin thread-like reticulation, 6 were almost BN. with only 1 or 2 flecks of white and 4 were completely BN.

An F_3 of 66 was given; they were examined as they were approaching maturity, when 54 were found to be practically normal, 1 RB., 3 with very thin reticulation, 4 almost BN. and 4 quite BN. Two matings were made with the Black Nowhites crossed with the genotypic BN. of *D. XIII*, and one with the phenotypic Nowhite of *D. XVI*. All the offspring were normal-eyed Black.

D. LI.

Nowhite not proved. In the F_2 4 BN. and 2 HN. were given, all from the intermatings of one F_1 brood. 2 BN. and 2 HN. came from mixed matings in the brood-bowl; the other 2 BN. from a pair out of the same bowl. (They had young as follows: 3 B.; 7 B., 1 BN.; and 8 B., 1 BN.) All six were unchanged at maturity, but none survived to breed.

D. LV. Phenotypic Nowhite.

Out of an F_1 of 48, only 3 males and 7 females survived to breed. The offspring from the different matings were all normal-eyed Black with the exception of 4 broods from *Pair 2*, viz. 6 Black (1 spd.) all with thin reticulation; next 8 B. (1 spd.), 1 BN.; 2 B. (1 spd.); and 4 B., 2 BN., a total of 20 Black and 3 BN.

Only 4 of the Black normals reached maturity, 2 ♂♂ (one→HN. left eye) and 2 ♀♀ (one→HN. right eye→BN.).

The HN. ♂ and ♀ mated and gave 1 brood of 3 B. normals (1 spd.) (died). The normal-eyed mated, giving 40 Black (2 spd. and 1 thin retic.); and mixed matings had 14 B. (2 spd.) and 1 HN. left side (the HN.→BN. ♀ and died).

The 3 *Black Nowhite*→♂♀♀. The male mated with one female and had 2 broods, 9 B. normal-eyed (1 spd.) *D. 3090*; with the second female, 1 brood of 3 Black (1 almost nowhite) and 3 BN. (*D. 3138*, all died). This female was then tried with one of the normal males and gave 1 brood of 1 B., 1 BN. (→BN. ♀).

She was tested with a genotypic Nowhite from *D. XIII* stock, and gave 3 broods, 8, 10 (1 spd.) and 10 (2 spd.), all Black normal-eyed.

In the F_3 there were 4 survivors of the *D. 3090* brood, 2 ♂♂ and 2 ♀♀, all with greatly reduced pigment; one pair giving 1 B., 1 HN. (*D 3216*), and the other a brood of 2 BN. (D. 3217).

These 2 BN.→♂ and ♀ mated (the third BN. mating in the stock) and had 1 brood of 3 Black (2 spd.) normal-eyed but with the reticulation rather thin.

D. LXI.

Nowhite not proved. 62 F_1 were hatched in 3 broods. One brood gave offspring, 26 B., 3 BN., 2 HN.; the second, 64 B., 5 BN. and 3 HN.

The third brood had only 1 survivor, a male evidently cannibal. The Nowhites and Half Nowhites remained unchanged, but none reached maturity. The normal-eyed matings gave an F_3 of only 6 Black normals.

D. LXIII. Gradual Nowhite ?

Six of the F_1 at maturity showed a great reduction of pigment, 2, ♂ and ♀, reaching the completely nowhite stage.

These two, *Pair 1*, gave 1 brood of 6 Black normal-eyed, but in a mating with another male (normal→thin reticulation) the female hatched a brood of 9 B. (3 spd.), 3 BN. and 2 almost BN. All the F_2 died immature.

D. LXVIII. Phenotypic Nowhite.

The F_1 numbered 30 B. and 5 BN.—but it must be noted that 10 of the Black and the 5 BN. were not examined until they were two months old, and though they may have hatched BN., yet the possibility of their being normals→BN. cannot be overlooked—one of the 10 normals became BN. at maturity.

Seven males, 6 B., 1 BN., and 14 females, 11 B., 3 BN., reached maturity. The BN. male and 3 females mated in the brood-bowl and gave 7 B. normal and 4 BN. young. The male died and the females were tried with normals of their own brood. One mating B. ♂ × BN. ♀ had 66 B. (3 spd.), 8 BN. and 2 almost BN.; another of the same type produced 17 B. (3 spd.); one normal B. pair gave 18 B. (1 spd.), 1 BN. and 3 almost BN.; the other normal matings had normal offspring only.

The Nowhite was tested by crossing with the genotypic nowhite of *D. XIII*, Black normal-eyed young resulting from the mating.

V. *Changes in retinal pigment.*

There were several instances in the experiment of the changes in the retinal pigment, 6 Red-eyes and 1 new variant type, near to the Lilac-eye.

In *D. VIII*, *XVIII* and *XXIX* it was not possible to prove the constitution of the recessives owing to their scarcity and delicacy, except that in *D. VIII* the r_1 or r_2 genes were shown to be absent.

The r_2 gene reappeared in four other stocks, in *D. XXXI A.* and *XXXI*, carried by the female; in *D. XLVI* probably by the male; in *LIII A.*, where it appeared in the F_1, by both male and female; in *LIII*, *LIII* (2), *LIII* (3) by the female; and in *LXIV A.* and *LXIV* by the female.

D. VIII. Red-eye recessive, not r_1 nor r_2 gene.

Out of 58 F_1 33 survived to maturity, 10 males, 1 male (?) and 22 females. 7 males only were effective, and were mated first with females from their own brood-bowls, and six of them later with other untried females. One pair out of them all gave Red-eyed young amongst the Black, 59 B. to 18 R. The male of the pair was mated with another female, and 16 B. young were produced, but all died immature.

There were only 9 survivors of the Reds, all males. They were tested with the Red Nowhite of Stock I and with the Red of Stock II, and proved distinct from both.

The Black intermated, but only a very small F_2 was given, 36 all Black.

The Red factor was probably introduced by ♂ *VIII*. The female gave only Black in her "Outside" mating, and in another Inside mating, with ♂ *IV*, an F_1 of 42 B., and F_2 56 B.

D. XVIII.

Red-eye recessive, not proved. Two out of eleven families gave some red-eyed in their offspring, but, counting the individuals proved for the red factor, eight were heterozygous, and one of these, ♀ 11, gave Nowhite as well.

The numbers were as follows in the broods: 12 B., 2 Red; 2 B., 1 Red; 7 B., 3 Red; and 4 B., 1 Red.

The colour was a clear bright red, more concentrated in the lower part of the eyes, with no tinge of darker pigment. It remained unchanged, but unfortunately the gene involved could not be tested as the only two males which came to maturity, and were mated, died without giving any offspring.

D. XXIX.

Red-eye recessive, not proved, and *Irregulars*. Five F_1 broods were hatched.

In the first brood of 16 Black, one animal had its head malformed on the right side, the right eye very irregular, and the white reticulation much broken→♂. Later, two others in the brood developed the same malformation→♀♀. The male and one of these females were put together as *Pair 1*, and had 21 normal-eyed B. young; the second female mated with a normal B. male, and hatched 28 normal-eyed Black. The survivors were all normals.

Twenty-five F_1 pairs were set out, 19 proving effective and 9 mixed matings. Only 2 of the pairs gave Red-eyed offspring, *Pair 8* and *Pair 14*.

A peculiarity in this strain was an irregularity in eye-structure, especially in the left eye—7 Black (6 Left, 1 Right) and 4 Reds (2 Left, 2 Right) which occurred in several broods. It varied in degree from a slight change in shape to the extreme cases in which the ommateum was broken up, with patches of ommatidia lying outside and separate from it.

The details of the appearance of the Red and the Irregularity are as follows:—

From *Pair 5*, 7 broods; the fifth consisted of 8 Black, with thin broken reticulation, 1 almost nowhite with a large very irregular Left eye, in two separate nowhite portions, divided transversely by a bar of white pigment.

From *Pair 7*, 3 broods; the last, of 1 Black with a very irregular Left eye, with separate patches of ommatidia.

From *Pair 8*, 7 broods; the second (*679*) was composed of 6 Black and 1 Red; the third (*693*) of 11 Black (4 spd.) and 5 Red; the fourth (*1098*) of 7 Black, 4 of them very reddish and irregular; the other broods were normal-eyed Blacks.

Brood 679. The Red-eyed specimen had an irregular, much broken-up Right eye, part nowhite. Died immature.

Brood 693 just extruded. All with more or less irregularity, and varying quantity of white pigment, and only one or two of the Blacks fairly normal. Many of the Blacks were very reddish, and 1 had an irregular Left eye drawn out behind. The Reds were the faded red colour, characteristic of this appearance, 3 of them with irregular eyes, 2 Left and 1 Right.

Brood 1098. The 4 irregular-eyed Black had patches of ommatidia almost separate from the ommateum, 3 Left eye and 1 Right. All died.

From *Pair 14*, 2 broods, 1 of 5 Black and 1 of 1 Red-eye.

There were 7 Reds altogether, but unfortunately their constitution could not be proved as none lived to maturity.

The colour was a distinct clear red without any admixture of the dark pigment, rather more dilute than the shade we call "normal red," and in consequence less brilliant and more faded looking. It did not change with growth.

The Black matings failed, only 4 F_3 being produced before the stock died out.

D. XXXI A. and XXXI. Reappearance of the r_2 gene.

The brood from the Outside mating of ♀ *XXXI* numbered 15 (1 spotted and reddish). All survived to maturity, and 6 pairs were set out in addition to mixed matings in the brood-bowl. Two of the pairs, *1* and *2*, gave red-eyed in their offspring, and ♀ *4* also proved heterozygous. Two other males, *4* and *6*, were found to be homozygous, but the rest died before their constitution could be tested.

The Red was proved to carry the r_2 gene, and to belong to the "unstable" class of eye-colour, but with no great range of colour, from bright Red to cream or Flushed white.

The results given by the heterozygous pairs are interesting for comparison.

Pair 1, 5 broods, 46 Black (3 BN. at birth and 5 almost BN. all→quite normal later) and 17 Red. The Reds were a pale clear bright red on hatching, and remained so through life.

Pair 2, 4 broods, 16 Black and 4 Red. All 4 were the palest cream colour at birth, and developed only a faint pink in 2 or 3 central ommatidia, though their young, some produced by mating in the brood-bowl, and others with the mates of the same type of colour from another r_2 stock (*D. LXIV A.*), all had bright red eyes.

The heterozygous male *2* was mated with ♀*4* (which had given 33 Black with ♂ *4*) and gave 12 young, 5 B.; and 5 Black and 2 Reds, the same coloration as the *Pair 2* offspring.

The Red-eyes from the Inside mating of ♀ *XXXI* appeared from matings in the very irregular *D. 151* brood—a pure red, pale and clear.

Pair 20 had 7 broods: 12 Black, 1 Red; 3 Black, 1 Red; 3 B.; 5 B.; 4 B.; 14 B.; and then again 9 Black and 2 Red. Descendants of these are still living.

The male of *Pair 20* was mated with the F_1 female (of his first brood) and gave 4 B.; 4 B. (1 spd.) and 2 Red; 2 B.; 7 B.; and 2 B.

Another pair had 1 brood, 6 B., 4 BN. and 1 Red—no survivors.

D. XLVI. Reappearance of the r_2 gene.

The ♀ had three matings: (1) With an Outside ♂, 1 brood of 13 Black (3 spd.); survivors, 3 females. (2) With a male of the same dredging, Inside mating, offspring 29 Black (2 spd.); survivors, 4 males, 5 females. (3) With ♂ *D. XX*, giving 19 Black (1 spd.); survivors, 3 males and 9 females.

The two Inside matings are treated together here. The factor for Red-eye was evidently carried by the ♀ *XLVI*; both matings gave red in the F_2 when mated *inter se* or when crossed together. An F_2 of 175 Black and 18 Red was produced.

The Reds were proved and found to carry the r_2 gene, and to belong to the "unstable eye-colour" class. The colour at birth varied from bright clear red to almost white, in the same family, but the changes and fluctuations with growth were remarkable. Nine were born with bright red-eyes, 4 survivors, pale pink, almost white; 9 were pale primrose, or a faint pinkish shade, 3 survivors, full clear red at maturity.

The proportions of black to red in the broods giving the recessives were as follows:—

Pair 1. ♂♀♀, 8 B., 2 Red pale; 3 Black.

Pair 4. ♂ and the 2 ♀♀ of *Pair 1*; 12 B. (1 spd.), 3 Red pale.

Pair 4. ♂ and ♀, 2 B., 3 Red (primrose); 12 B. (1 spd.), 3 Red (1 spd.); 6 B. (1 almost BN.).

Pair 4. ♂ and 2 ♀♀ (*226*), 39 Black, 4 Red bright; probably one of the females gave Blacks only.

The 2 ♀♀ (*226*) with another ♂ of their own brood ; 1 brood, 3 B., 3 Red (2 bright, 1 pale).

All died without offspring, except the male which was crossed with a ♀ from *dd. LXXIII* (r_2 gene) and gave 3 broods of bright Red-eyed, 11, 18 and 2.

D. LIII A. Reappearance of the r_2 gene. (**2**, p. 27.)

The brood of the heterozygous ♀ *LIII* in her Outside mating consisted of 9 Black (2 spd.) and 2 Red (1 spd.), showing that the male with which she had mated in the wild was heterozygous also.

This was the first time we had had colour changes in the F_1 from the wild, and the first *direct* proof of heterozygosity existent in the wild population (see p. 355). The Red colour in these and in the F_2 reds was pale and clear, but altered later, some gaining in intensity, others losing.

LIII.

The parent female in her Inside mating gave 62 Black (3 spd.) in 2 broods.

LIII (2).

She was then mated with ♂ *D. LXX*, and gave 1 brood of 37 Black. *LIII* (3) then with ♂ *D. LXI* and had 34 Black young in 2 broods. All 3 matings gave Red-eyes in the F_2 generation.

The colour in the recessives covers a greater range than in the Main Stock II, or in any of the other reappearances of the r_2 gene, from colourless, which developed faint lemon, pink or red tints, through all shades of red and lilac to deep ruby and purple. The interommatidial pigment also varies extensively from normal reticulation, thin reticulation, to sub-white and nowhite.

The experimental work on this stock is not yet finished, and the results therefore cannot be included here, but will be discussed in a later paper.

D. LXIV A. and *LXIV.*

Reappearance of the r_2 gene " unstable eye-colour division " proved by crossing with Stock II Red (*D. XXXI A.*).

The Red factor was evidently carried by the female parent ; it appeared in the F_2 of both her Outside and Inside matings.

LXIV A.

The mixed matings in one of the brood-bowls gave 3 broods ; 12 B. (3 spd.), 1 Primrose ; 6 B. (1 spd.) ; and 13 Black (1 spd.), 2 Primrose.

Although all three had eyes so pale at birth as to be almost white, the red pigment developed later, denser in the lower part of the ommateum.

Two survived, ♂ and ♀, and gave 1 brood of 3 Red-eyes like their parents with the pigment dense in the lower part.

In *LXIV*, the Inside mating, the F_2 numbered 323 Black (20 spd.) and 20 Red (5 spd.). Out of 9 effective pairs and about 15 mixed matings Red-eyes appeared in three instances; in one mixed mating 3 B. to 1 Red; in the offspring of *Pair 4*, 32 B. (1 spd.) to 17 Red (5 spd.); and in the mating of the male of *Pair 4* with the female of *Pair 5* (gave all B.), 12 B. (1 spd.) and 2 Red.

As is usual in the " unstable " division of Stock II Red-eyes the colour varied, from a pale pink to a bright full red.

D. X. New variant type.

This is a quite distinct stock, bearing a great resemblance to the Lilac Stock (**4**, p. 395) in the colour of the recessives, the two Lilac types, Creamy and Reddish, being represented; in the behaviour of the white pigment varying from heavy reticulation to Nowhite; and in the pale colour of the gonads and eggs. Whether or not it is genotypically the same, it is not yet possible to say, owing to the scarcity and low viability of the recessives.

The F_1 numbered 117 Black (3 spd.).

Mixed matings in the brood-bowls gave an F_2 of 131 (10 spd.), all of which were normal Black, with one exception, viz. 1 almost Nowhite, with very reddish black eyes. It died immature.

In addition to the matings in the bowls, 26 pairs were set out, but only 25 of the animals proved effective, giving the small number of 64 offspring, 58 Black, 6 Red-eyed.

The Reds came from two pairs, *Pair 10* and *Pair 15*, as follows:

Pair 10 had 2 broods, neither examined at birth, one of 4 Black (1 spd.); and the other, *D. 2727*, of 1 Black and 1 Dark Reddish Lilac Nowhite.

Pair 15 had 3 broods: one, *D. 1198*, examined when just extruded, of 2 Black (1 spd.) and 2 Dark Red.

One, *D. 2206*, examined within two days of hatching, of 3 Black (2 spd.) and 3 Dark Reddish Lilac Nowhite.

And one, *D. 2474*, of 2 Black, examined when about a month old. Taking the broods in order of time:—

D. 1198. The 2 Dark Red died within a short time of extrusion.

D. 2206. The red of the 3 Nowhites was a deep clear colour when examined on February 26, 1934, a day or two after hatching. By May 14, one only was left. It had a patch in each eye of 6 clear creamy yellow ommatidia thinly outlined in dark pigment, surrounded by a broad band of deeply pigmented reddish lilac ommatidia. Re-examined on June 14, the reddish colour had intensified to purple, and the creamy patches had clouded over but were still plainly visible.

On July 10 it was marked as "Nowhite ♂, eyes all over dark reddish purple, almost black; the clear spaces are now covered."

It was mated with a Black female from *D. 2727* which had pale eggs, and white mixed with the green of the gonads. Later, the eggs darkened to the normal dark green and the white in the gonads disappeared. A brood of 5 Black was produced, *D. 3108*.

Only one of the *D. 3108* young survived to maturity, a female, which was mated with an F_4 male from *D. X A.* (the Outside mating of ♀ *X*), as no male of her own stock was available. Two broods of 16 Black (2 dorsally spotted) were given, *D. 3192*, all with "heavy reticulation" (i.e. an excess of the white pigment), and from their intermatings the heavy reticulation in the Blacks, as well as the Dark Reddish Lilac type normals and nowhites, have appeared again, but so far none of the Creamy Lilac type.

D. 2727. 1 Black and 1 Dark Reddish Lilac Nowhite; about 3 to 4 weeks old when examined. In the latter there was a patch in the centre of both eyes of light yellowish ommatidia (like the Creamy Lilac) surrounded by a deeply pigmented Dark Red band along the front margin. The specimen died immature; examined after death, the dark surrounding band had intensified to black and the colour in the centre patches had also deepened, to dark yellow. The 1 Black became a ♀ and was mated with a *B.* ♂ of *X A.*, giving a brood of 5 Black (1 spd.), all with heavy reticulation, and 2 Reddish Lilac Nowhites. Examined when nearly mature, the colour showed as a clear bright red in the centres, surrounded by pale purple; as they grew older the colours deepened in tone.

The Blacks are now breeding and have given offspring, all so far with heavy reticulation, and several spotted.

VI. *Irregularity.*

(*a*) *Irregularity of eye-shape.*

Irregularity was of frequent occurrence throughout the stock, but usually appearing sporadically not often in successive generations.

The stocks are as follows :—

D. VIII A. F_1: 1 very irregular, spotted and reddish at birth, →Black.
D. VIII F_2: 1 irregular and almost Nowhite.
D. IX A. F_1: 1 very irregular, Right eye, only 2 ommatidia.
D. XI A. F_2: 1 very irregular, Left eye.
D. XII F_2: 2 irregular and malformed heads (1 R.S. and one both sides).
D. XV F_2: 1 very irregular, Left eye.
D. XX F_1: 2 irregular malformed →practically normal-eyed and gave normal-eyed young.

D. XXIII A. F_1: 1 irregular, Right eye.

D. XXIV F_2: From 1 pair, which gave 48 B. offspring; in one brood of 8 all almost BN., 2 very irregular in both eyes; in another brood of 7 B., 1 irregular in Left eye and spotted.

D. XXIX (see p. 339) F_1: 1 with malformed head, 2 normals→malformed; great irregularity in the stock.

D. XXXI.

This stock is peculiar for the appearance of an extraordinary variety of eye-irregularity in one brood of the F_1. The brood (*D. 151*) consisted of 21 normal-eyed Black (3 spd.) and 9 irregulars. No two of these were alike, some had the eyes divided in separate pieces, others looked as if different pieces had been joined together, some had one eye much larger than the other, some were flattened, others constricted in the middle, whilst many had the ommateum outline broken and black streaks or spots outside the margin. All 9 came to maturity and were mated, 8 in 4 pairs and the ninth, a female, with a brother male of the same brood. All the matings produced young with perfectly formed normal Black eyes, and curiously enough, none of the parents' irregular types reappeared in this, or in the following generation, from their intermatings.

D. XLIII.

Two F_1 females gave irregulars. One produced only 1 Black young with an irregular Right eye, and normal Left eye at birth. The Right eye was very wide with two portions carrying ommatidia separate from the ommateum. By the time maturity was reached the two pieces had joined together vertically and coalesced with the eye, giving it an extraordinarily broad appearance; the Left eye had also become irregular with small pieces of one or two ommatidia each, separate. The animal was a female, and was mated to a normal-eyed male. One brood was produced of 6 normal-eyed Black (3 much spotted), one with a deep sub-white dorsal patch.

In the second instance, the female had 24 Black young, 12 of them with many spots and 1 with a normal Right eye and a very irregular much larger Left eye with a large piece "broken off" on the top margin.

D. LVI F_2: 1 BN. malformed and much spotted.

(*b*) *Irregularity in body and gonad colour.*

Though the genotypic White-body type did not appear in this experiment, a certain amount of variation and lack of colour in body and gonads occurred scattered through the stock. "White-eggs" had been noted before in the Lilac Stock, but in the cases recorded (**1**, p. 202) the body and gonads were the normal green shade, i.e. the eggs formed in the ovaries showed as dark green, though when they were extruded from the oviducts into the pouch they were pearly white, and always infertile.

In the " White-eggs " females of this experiment the eggs in the ovaries were translucent white, in startling contrast to the green body colour, but by the time they had reached the pouch they had become tinted a pale nile-green shade, and were fertile. Some instances are given below :—

D. III (3).

Two F_1 females in one brood-bowl had " white-eggs " in the gonads. Microscopically examined later, one was found with the contents of the ovaries part white and part green, and the other with all green. Both extruded normal-coloured fertile eggs.

D. XVI.

In one F_1 brood-bowl, 7 females matured, 2 with " white-eggs " and 5 with dark green. When examined, 1, a Black Nowhite, had just extruded a batch of eggs into the pouch, a very pale green tint, not the normal dark colour. The second female gave no offspring.

D. XXII.

Out of 8 females in one F_1 brood, 3 had " white gonads " and 5 dark green. Two died without mating, the third gave the pale green eggs, fertile.

D. XXXIX.

The F_1 took an exceptionally long time to mature, and only 13 survived out of 71 hatched. They varied greatly in size, some looking as if they came of another generation. Five, 2 males and 3 females, had the typical *White-body* appearance, with no tinge of colour in body or gonads at maturity. It was found to be quite definitely *not* the same as the genotypic White-body (described in **4**, page 374), for while the body remained white through life, a certain amount of colour developed in the gonads and eggs. It proved impossible to trace the inheritance of this variation owing to the dwarfing, the high mortality and the difficulty of finding " white-body " animals suitable in size to mate together (only 3 of such matings were obtained) or with normal-body. There seemed to be some sort of hereditary factor running through the generations, as will be seen from the instance given below from the first " white-gonad " female to mature.

This female reached maturity at the age of six months, and was put with a male from the same brood, January 10, 1934. Both were pearly white, body and gonads. The ovaries showed as rows of round translucent white eggs. On February 4 it was noted that a pale shade of nile-green could be seen in the ovaries under the microscope. May 2, a brood of 2

Black young, both white-bodied (*D. 2411*), was hatched and new eggs laid, green in colour, but not the blackish green of the normal eggs. On June 26, again examined microscopically after another brood had hatched 3 Black (*D. 2850*), it was seen that the ovaries contained green eggs, mixed with the white ones. The ♀ was examined at intervals after broods were extruded, and it was found that more and more of the eggs formed in the ovary were coloured, and that the eggs laid were darker, though the colour concentration of the normal was never reached, and that as they ripened in the pouch they were yellow, much paler than the usual orange tone.

This pair gave 39 Black young, but only 2 survived, a normal-body male from *D. 2850* and a white-body female (*D. 2411*). The latter was mated with a white-body male and gave 2 white-body young (*D. 2924*), one of which became a female and was put with the normal body ♂ *2850*. At the time of maturity 16 " white-eggs " were counted in the ovaries. The eggs when laid were examined microscopically and were seen to be lying in 4 rows of two in a row in the pouch, the first 2 very small, the next 2 three times the size, the next a little smaller and the last 2 smaller again. Four young were hatched (1 spd.), " pale body-colour but not white-body " (*D. 3060*); they did not survive to maturity, but the colour was unchanged at 4 months age.

D. XLII.

One F_1 female out of 19 survivors (12 ♂ and 7 ♀) had the appearance of "White-body." There was no tinge of colour in the body, but the eggs laid were the dark green normal tint. In the F_2, 3 animals out of a brood of 17 were very white, 2 males and 1 female, but were not White-body, the female having pale-coloured gonads. Died without offspring.

INCUBATOR CONDITIONS (Table III).

I. *Temperature and Development.*

The *temperature* in the Incubator was approximately 21° C., only rising slightly at midday, and in the coldest weather dropping a little in the early hours of the morning. The average of the daily readings (recorded on the thermograph) at 10.30 a.m. ranged from 20·13° to 20·8° February to April, 1933, 21° to 21·75° May to September, and 20·75° to 20·13° October to December.

Development.

F_1. The time taken by the parents from the wild for the eggs laid in the Incubator conditions, counting from oviposition to extrusion of the broods, was practically constant, 9 days being the usual period for all (very occasionally 10 days).

TABLE

INCUBATOR CONDITIONS.

OUTSIDE MATING.

	F_1			F_2
Stock No.	Black.	Spotted.		Black.
DD. I	1			—
DD. II	No eggs			—
DD. III	,,			—
DD. IV	2			—
DD. V	No eggs			—
DD. VI	Eggs thrown off			—
DD. VII	No eggs			—
DD. VIII	,,			—
DD. IX	15			118 B. and 1 RB. very reddish and sl. irreg.
DD. X	Eggs thrown off			—
DD. XI	No eggs			—
DD. XII	,,			—
DD. XIII	,,			—
DD. XIV	,,			—
DD. XV	13	12	survivors 2 ♂, 8 ♀	12
DD. XVI	20	2	1 ♂ 2 ♀→thin retic.	201 (43 spd.)
DD. XVII	23	2		151 B., 3 BN. spd., 3 HN. spd. (BN. and 1 HN. irreg.). *Nowhite*, not proved.
DD. XVIII	3 heavy retic. and 2 spotted			—
DD. XIX	24	5	1 ♂→sl. irreg.	25
DD. XX	Eggs thrown off			—
DD. XXI	No eggs			—
DD. XXII	,,			—
DD. XXIII	,,			—
DD. XXIV	,,			—
DD. XXV	,,			—
DD. XXVI	,,			—
DD. XXVII	Eggs thrown off			—
DD. XXVIII	,, ,,			—
DD. XXIX	1			—
DD. XXX	No eggs			—
DD. XXXI	Eggs thrown off			—
DD. XXXII	,, ,,			—
DD. XXXIII	,, ,,			—
DD. XXXIV	No eggs			—
DD. XXXV	,,			—
DD. XXXVI	,,			—
DD. XXXVII	,,			—
DD. XXXVIII	,,			—
DD. XXXIX	,,			—
DD. XL	,,			—
DD. XLI	,,			—
DD. XLII	32	12	Survivors, 12 ♂, 8 ♀	111
DD. XLIII	17	11		2
DD. XLIV	23	3		—

III.

D EXPERIMENT.

INSIDE MATING.

Stock No.	F_1 Black.	F_2 Black.
dd. I	201 B. and 8 B. irreg. (5 ♀ irreg. out of 9 in 1 brood)	227
dd. II	85 6→thin retic.	23
dd. III	70 *Gradual Nowhite*	35 B., *1 HN. spd.
dd. IV	50	—
dd. V	110 2 ♀→RB.	26
dd. VI	127 (27 spd.)	141 B., 1 HN. spd.
dd. VII	62	45
dd. VIII	123 B., *1 HN., 5→almost BN.	49 B., 2 BN., 2 HN. *Nowhite*, not proved.
dd. IX	118 B., *2 BN. spd., *7 HN. spd. (1 ♂→ BN.) *Spotted Nowhite*	10 B., *1 HN. spd. In F_3 17 B. and *1 HN.
dd. X	140	23 B., 1 HN. spd.
dd. XI	117	184
dd. XII	94 1 ♀→BN., 4→alm. N.	144 B., 1 BN., 1 HN. irreg.
dd. XIII	91	15
dd. XIV	104	—
dd. XV	142	—
dd. XVI	110	—
dd. XVII	68	123 B., 1 BN. spd., 1 HN. spd.
dd. XVIII	84 (21 spd.) 1 ♂ →alm. BN.	—
dd. XIX	126	—
dd. XX	81	147 B., 16 BN., 1 HN. *Nowhite.*
dd. XXI	44	—
dd. XXII	152	—
dd. XXIII	147	60
dd. XXIV	55	23
dd. XXV	54	10
dd. XXVI	124 Parents irreg. eyes and ♀ "clotted"	50
dd XXVII	16	—
dd. XXVIII	172 B., *1 BN. spd., *9 HN. spd. *Spotted Nowhite*	84 B., *1 BN., *2 HN.
dd. XXIX	46	—
dd. XXX	62	—
dd. XXXI	49	-
dd. XXXII	96 1 ♂→alm. BN.	3 B., *1 HN.
dd XXXIII	37 B., 1 HN.	—
dd. XXXIV	19 1 ♂→alm. N.	-
dd. XXXV	30	—
dd. XXXVI	8	—
dd. XXXVII	90	—
dd. XXXVIII	57	—
dd. XXXIX	42	2 B., *3 BN., *1 HN. **Red-eye recessive** (7 : 6, 18 : 4), prob. F_3.
dd. XL	23	—
dd. XLI	39 B., *1 BN. spd., *1 HN. spd.	120 1 heavy retic., 1 thin retic.
dd. XLII	38	9
dd. XLIII	94	180 B., 1 RB., **18 Red, Red-eye recessive** (r_2) 1 irreg.
dd. XLIV	35	—

* Not examined at birth.

TABLE III

OUTSIDE MATING.

Stock No.	F_1 Black.	F_1 Spotted.		F_2 Black.	
DD. XLV	14	6		14	
DD. XLVI	15	1		—	
DD. XLVII	No eggs			—	
DD. XLVIII	9	2	*Gradual Nowhite*	6	
DD. XLIX	Eggs thrown off			—	
DD. L	19	2		—	
DD. LI	No eggs			—	
DD. LII	20		3→alm. BN.	8	
DD. LIII	11	3		—	
DD. LIV	10			—	
DD. LV	18	9	*Gradual Nowhite*	—	
DD. LVI	10	2		—	
DD. LVII	22 B., 1 HN., 4 spd.			—	
DD. LVIII	No eggs			—	
DD. LIX	1			—	
DD. LX	No eggs			—	
DD. LXI	19	7		—	
DD. LXII	22	6	*Gradual Nowhite*	14	
DD. LXIII	16	9		—	
DD. LXIV	No eggs				
DD. LXV	13	8 spd. (7 dorsally)		36	(9 spd., 6 dorsally).
DD. LXVI	Eggs thrown off			—	
DD. LXVIII	44	4	1 ♀ × ♂ from *dd. LXVIII* gave	28	
DD. LXIX	14	2		8	
DD. LXX	19			—	
DD. LXXI	22	8	1 ♂ 4 ♀ survivors	42	(16 spd.).
DD. LXXII	36	1		—	
DD. LXXIII	27			31	
DD. LXXIV	12	1		7	
DD. LXXV	20	2	2 ♂♂→alm. HN.	33	
DD. LXXVI	28			5 B., *3 BN., *3 HN.	*Nowhite* not proved.

* Not examined at birth.

—*continued.*

INSIDE MATING.

Stock No.	F_1 Black.		F_2 Black.	
dd. XLV	66		—	
dd. XLVI	102		—	
dd. XLVII	22		—	
dd. XLVIII	60		—	
dd. XLIX	36		40	
dd. L	51		—	
dd. LI	5		—	
dd. LII	52		—	
dd. LIII	73		—	
dd. LIV	19		—	
dd. LV	66	♂ parent heavy retic.	9	BN. spd., probably F_3.
dd. LVI	37		—	
dd. LVII	48		—	
dd. LVIII	58		—	
dd. LIX	52		4	
dd. LX	47	B., *4 BN. spd., *3 HN spd. (1 BN. and 2 HN. irreg.). *Spotted Nowhite*	177	
dd. LXI	52		—	
dd. LXII	88		—	
dd. LXIII	21		1	
dd. LXIV	90		34	(8 irreg.-eyes).
dd. LXV	79	(13 survivors of 1 brood were all ♀)	—	
dd. LXVI	87		8	RB., 1 alm. Dark Red.
dd. LXVIII	38		*8	RB. (3 alm. DR. Gave B. (2 irreg.) in F_3.
dd. LXIX	27		21	2 irreg.
dd. LXX	17		13	B., 2 RB., **6 Red. Red-eye recessive** (r_2).
dd. LXXI	39		47	1 irreg., 2 "clotted."
dd. LXXII	25		—	
dd. LXXIII	42	1 *Half-Red*	538	B., 2 HN., **71 Red. Red-eye recessive** (r_2). Reduction of white pigment.
dd. LXXIV	35		12	B., *1 BN.
dd. LXXV	2	Parent ♀ heavy reticulation	—	
dd. LXXVI	76	Reduction of white, 1 ♂ "clotted"	107	B., *2 HN.

* Not examined at birth.

The age at which the F_1 became mature and started breeding varied greatly, the average for the first 3 months was from 75 to 80 days, but there was no uniformity. The shortest time was in 42 days, the longest recorded was 131, but other broods hatched at the same time as this took 56, 62, 70, 80, 84, 86, 88 ; one brood matured at 3 months but did not begin breeding till 5 months old ; another brood was not yet mature at 5 months.

It is remarkable that the development of the F_1 incubator young should in many instances take the same length of time as the F_1 in the "Natural Conditions" part of the experiment. Some of those in the heat hatched in 9 days in March and became mature at 5 months ; those in the cool laid during the same period took 34 to 36 days to hatch and 5 months to develop. In April, broods hatched at the same time after 9 days' incubation in the heat, and 23 to 25 in the cool, reached maturity in the first case at 52 days, 4 months, and 4½ months, and in the second case at 69 days, 4 months, 4 months and 5 months.

F_2. The F_2 broods took on the average 9 to 10 days to hatch ; a few in July and August at 8 days ; only one record of 7 days, in May.

Owing to the great mortality, a large number did not reach maturity, so that there are not many records for the age of F_2 parents at the time of their first oviposition. To take one stock only, *dd. LXXIII*, the age in days varied from 37 to 74, the first mentioned being from a brood extruded on July 5, and the last from a brood extruded July 24. An August brood was 68 days old when mature and was not breeding even then.

II. *Variations in the Interommatidial Pigment.*

An interesting point in the Incubator experiment is the number of stocks in which variations of the interommatidial pigment occurred, all tending to reduction of the amount of white normally deposited in the embryonic eye.

Where such cases occurred in the "Natural Conditions," the tendency was for the amount to be made good by a rapid increase in the rate of deposition bringing the white up to the normal in the early growth-stages, but no such increase took place in these Incubator stocks.

Nowhites and Half Nowhites were frequent, but unfortunately their constitution could not be tested owing to the high mortality.

Spottedness was another feature, i.e. excess of the white pigment, as shown in spots and patches apart from the eye.

Twenty-five cases of slight Irregularity in eye-shape were also noted, in the BN., HN. and normals, and 3 Clotted-eyes were found.

The details are as follows :—

dd. III. Gradual Reduction, probably a Case of the Gradual Nowhite.

In one F_1 brood 26 Black were hatched normal-eyed on extrusion. 11 survived, but developed very slowly; microscopically examined at the age of 4 months, all were still small, only 3 males and 4 females were mature; all showed reduction of the white pigment. Seven weeks later the only survivor, a female, had become completely Nowhite. The young from the intermatings in this bowl numbered 11 B. normal-eyed and 1 HN. spotted. None survived.

dd. IX. Half Nowhites.

One F_1 brood was remarkable for the number of Half Nowhites in it; out of 30 hatched, 2 were BN. and 7 HN., 3 with the left eye nowhite and 4 with the right eye, and all the 9 were spotted (3 dorsally). None survived.

DD. XVI. Spottedness.

The F_1 "Outside" brood numbered 20 Black (2 spd.), of which 5 males and 8 females survived, 3 with a slight reduction of pigment. An F_2 of 201 was produced with 43 spotted, but 25 of these came from 1 female, mated with 2 different males. With the first she gave 13 spotted out of 17, and with the second 12 spotted out of 23.

DD. XVII. Spotted Nowhites.

Six appeared in the F_3, 3 BN. and 3 HN. all spotted, and 3 of the BN. and 1 HN. had irregular-shape eyes also.

The Nowhite was probably brought in by the female, as in a mating with another male 1 BN. and 1 HN., both spotted, appeared in the F_2. None reached maturity.

dd. XVIII. Spottedness.

In the F_1 21 were spotted out of 84 Black. No F_2.

dd. XX. Nowhite, not proved.

The three F_1 broods totalled 81 B. normals (5 spd.). Nowhites appeared in the F_2 in the offspring from two of the broods; in *Brood 23* 1 BN. from the mixed matings in the bowl and 8 BN. from one pair; in *Brood 72* 4 BN. and 1 HN. from mixed matings, and 3 BN. from one pair. None survived to mate.

dd. XXVIII. Nowhite, not proved.

The curious point about the F_1 from this pair was the appearance of a large number of Half Nowhites in the sixth and last brood. The numbers were: 24 B.; 38 B. (1 spd.); 24 B.; 42 B. (1 spd.); and 20 Black normals (13 of them spotted), 1 BN. spotted and 9 HN.

The only F_2 from the BN. and HN. matings were 2, 1 BN. and 1 HN., both spotted. The offspring from the normals and the other broods numbered 84 normals (3 rather thin reticulation) and 1 HN.

DD. XLVIII. Gradual Reduction, probably the Gradual Nowhite Variation.

The Outside brood consisted of 9 Black (2 spd.), of which 4 survived—1 ♂→almost Nowhite, 2 ♂♂ almost Half Nowhite and 1 ♀→ thin reticulation. Mixed matings gave 6 B. normal-eyed young. None survived.

DD. LV. Gradual Reduction.

The Outside brood numbered 18 B. (9 spd.). There were 8 survivors—1 ♂ and 1 ♀→BN., 2 ♂♂, ♀ and 3 nearly mature became almost Nowhite. No young were produced.

dd. LX. Nowhite, not proved.

This stock is like *dd. XXVIII* both in the appearance of Nowhites and Half Nowhites in one brood out of six, and in the large proportion of spotted in the same brood. The first brood numbered 8 B. (3 spd.), the second 15 Black normal-eyed (of which 13 were spotted), 4 BN. spotted, and 3 HN. spotted. The Nowhite did not reappear in the next generation.

DD. LXII. Gradual Reduction, probably the Gradual Nowhite Variation.

This Outside brood took 4 months to reach maturity. There were then 3 males and a female with thin reticulation, one male practically BN. They gave 14 B. normal-eyed young.

DD. LXV. Spottedness.

A remarkable number of spotted must be noted here as coming from a mating in the wild, 8 out of a brood of 13 being spotted (of which 7 were in the dorsal position). In the F_2 there were 9 spotted in a total of 36, 6 being dorsal.

dd. LXXVI Gradual Reduction.

Out of an F_1 of 76 Black, 1 ♂→ almost BN.; 1 ♂ and 2 ♀♀ → thin reticulation, and 1 ♂ had rather "clotted" eyes.

In the F_2, 2 HN. appeared out of 109 animals (1 thin reticulation). The F_1 from the Outside mating of the same ♀ numbered 28 Black normal, and gave an F_2 of 11, viz. 2 ♂♂ and 2 ♀♀ normal; 1 ♀ almost nowhite; 1 ♂ with only a trace of white in the left eye, right eye nowhite; 1 ♂ and 1 ♀ with right eye Nowhite; and 2 ♂♂, 1 ♀ completely Nowhite.

III. *Changes in retinal pigment.*

Four of the stocks gave Red-eye recessives in the F_2 generation. These were tested, and all were found to carry the r_2 gene, and to belong to the "stable eye-colour" category.

dd. XXXIX Red-eye recessive (r_2).

F_1 consisted of 42 Black normal-eyed. From mixed matings an F_2 of 2 B., 3 BN. and 1 HN. was produced, but as these were not examined until maturity, it is not known whether this is a case of nowhite at birth or of gradual reduction.

Some small young were found in the same bowl and judged to be F_3, 7 Black and 6 Red. Another brood from the same BN. ♀ in a bowl with 1 B. ♂ and 2 BN. ♂♂ numbered 18 Black and 4 Red.

Eight Reds survived, 7 males and 1 female, eaten later. One male became almost nowhite. One was tried with a Black female of the same brood and had 4 B. young. A second was crossed with a Red ♀ from *dd. LXXIII* stock and gave all Red young as would be expected, both carrying the r_2 gene.

dd. XLIII Red-eye recessive (r_2).

The F_1 numbered 94 Black. Three pairs survived of 1 brood and *Pair 3* gave 15 B. to 16 R. In another brood mixed mating gave 7 B., 2 R. A heterozygous B. ♂ of the F_2 was mated with a Red ♀ from *LXXIII* Stock and the Red was found to be the same constitution.

dd. LXX Red-eye recessive (r_2).

There were two small broods in the F_1, 12 B. and 5 B. respectively. From mixed matings in the first brood were obtained 10 B., 5 R. and from the second brood 3 B. ♂♂♂, 2 RB. (♂ and ♀) almost Dark R. and 1 R. ♀.

The Reds were tried with Stock *dd. LXXIII* and gave Red-eyed offspring. They were also crossed with Stock I Red Nowhite and gave Black.

dd. LXXIII. Appearance of a One-sided Red (r_2) *in the* F_1.

This is the second instance in the D. experiment of the appearance of a recessive in the F_1 from the wild (see p. 342, *D. LIII A.*).

The F_1 consisted of 42 Black normal-eyes, and 1 specimen a Half-Red, with the left eye black and the right eye bright red. It became a male and proved to behave genetically as a heterozygous Black. Mated with 2 heterozygous females, it gave 77 B. and 22 Red with one, 25 B. and 12 R. with the other. It was then mated with 3 F_2 Red females giving 11 B., 10 Red with one, 10 B. and 11 R. with the second, but with the third (from its own mating with one of the B. females) the proportions were 2 B. to 20 Red.

The occurrence of a " one-sided " animal, i.e. an animal with the two eyes different from each other, is not infrequent in *Gammarus chevreuxi*, although such a difference in the retinal coloured pigment as shown in this instance, is very rarely found.

Two other specimens in the experiment were noted as definitely One-sided Red or Half-Red at birth, viz. one in *D. IX* (p. 327) and one in *D. XXXIII* (p. 328), but these would appear to be in another category. Neither survived, but from the fact that a slight deposit of melanin was found in the Red eyes after preservation it seems probable that the red in these eyes was due to a slowing down or a temporary cessation of melanin deposition on one side, and that if the animals had lived, the melanin deficiency would have been made good later. In the *dd. LXXIII* specimen under discussion, the red of the eye remained unchanged through life.

In the white interommatidial pigment, on the other hand, there are many records of One-sided Whites, or Half-Nowhites (HN.), i.e. animals in which at birth one eye has the normal white reticulation, and the other none. Cases also of this peculiarity in relation to eye-structure have occurred in which one eye is regular in structure, and the other irregular (see p. 344 for examples).

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A Summary of the work on the Amphipod *Gammarus chevreuxi* Sexton carried out at the Plymouth Laboratory (1912–1936).

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INTRODUCTION.

The work began in June, 1912, simply as a study of the life-history of some of our common amphipods. The genus Gammarus was chosen, because of the number and the wide distribution of its species in the neighbourhood. Seven of these species, all black-eyed, from marine, estuarine, brackish and fresh waters, were kept in the laboratory for investigation until the first red-eyed specimens were discovered in one of the brackish species, later described as *Gammarus chevreuxi* (see p. 360). Since the manner in which these red-eyed individuals occurred raised points of considerable interest, it was decided to confine investigation to *G. chevreuxi*, and a series of experiments was started. The different variations involving both the structure and the pigmentation of the body and of the eyes appeared from time to time, some behaving as simple mendelian characters and attributable to the presence of a single recessive gene, others with a more problematical hereditary basis. These variations have been recorded as they occurred (see bibliography). For ten years, no second mutation appeared, although frequent dredgings were made and the animals thus obtained were kept for several generations in laboratory conditions. Because of this apparent stability of character the wild Gammarus was regarded as a homogeneous population until, in 1922, it became increasingly evident that the results showing in the laboratory cultures could only be explained on the supposition that many recessive factors must be present in the natural conditions.

The evidence steadily accumulated, but direct proof was very difficult to obtain partly because (as we found in our experience with the cultures) the recessive types are often less viable than the normal, and therefore probably less able to withstand the competition in the wild, and partly perhaps because we had no criteria by which to assess the influence of the laboratory conditions (changes of temperature, food, salinity, pressure, etc.) on the constitution of the Gammarus, and so could not decide whether a variation was caused by the inherent action of the recessive genes, or by the untoward environment producing a change in the action of the normal genes.

It was not until March, 1933, that direct proof of the existence of heterozygosity in the wild stock was obtained. A Black-eyed female, which had mated and laid eggs before being brought into the laboratory, hatched her brood a few days later, 11 young, of which 9 were Black-eyed and 2 were Red-eyed recessives (**39**, p. 27). Up to the present, however, only one Red-eye recessive has ever been captured in the wild (**47**, p. 836). This was on October 22, 1935, when one Red-eye was found in a dredging amongst 2,040 Black-eyed. None have appeared since that date although thousands of Gammarus were brought in afterwards for investigation.

The present paper gives a history of this Gammarus work, and of the many recessive characters and other variations affecting the structure and colour of the body and the eyes which have been detected from time to time in the laboratory cultures.

The signs and abbreviations used throughout the paper as descriptions of types according to their appearance are :—for the colours, **B**., Black ; **RB.,** Reddish Black ; **DR.,** Dark Red ; **Int. R.,** Intermediate Red ; **R**., Red ; **W**., White ; **A**., Albino.

For the " Nowhites," **N**. added to the colours, e.g. **BN**., Black Nowhite ; **AN**., Albino Nowhite : in practice this symbol is only used for animals which are recessive for the Nowhite factor, i.e. Mendelian Nowhites.

Spd., spotted, i.e. with spots of white pigment on the head apart from the eye. The numbers of spotted are recorded throughout the paper where figures for broods are quoted.

The sign → = became, e.g. RB.→B.

Letters and figures italicised and bracketed refer to the designation of the experiments and the brood numbers in the records kept at the laboratory.

Note.—The term " filial generation " is used to cover all the members of the same generation within a given stock, the numbers F_1, F_2, etc., indicating which generation in descent from the parent pair is being discussed.

CONDITIONS IN THE WILD.

Gammarus chevreuxi was first found* (June, 1912) inhabiting the ditches traversing a low-lying salt-marsh formerly part of the tidal estuary of the River Plym (**1**, p. 542). This land, reclaimed about a hundred years ago and known as Chelson Meadow, is enclosed on the river side by a long embankment, and drained by sluice-gates into the Plym. It was used as a race-course and was well-drained and kept in good order. The conditions at that time were very favourable to the increase of the Gammarus, with the water never above a certain level, food in abundance and few enemies. The worst to be endured was a very occasional drought, such as in the hot summer of 1911 (and again in 1921) when most of the ditches dried up, but even then shelter and moisture, sufficient to prevent the species being wiped out, could be found in places. The Gammarus population was at that time apparently a very stable one, consisting, generation after generation, of normal Black-eyed animals. Also, with the exception of the Red-eyed mutation referred to above (known later as Stock I Red-eye), not one of the many hundreds of pairs brought in from the wild gave anything but normal Black-eyed offspring.

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* *G. chevreuxi* has recently been found by Crawford (Journ. Mar. Biol. Assoc., XXI, No. 1, p. 102) in similar habitats on the coasts of Devonshire. It was recorded in 1931 by Pentelow from inland brackish waters, Wyken Slough, near Coventry (**20**, p. 797), an observation which has just been confirmed by Dr. R. W. Butcher. Other localities, on the French coast, are given by Chevreux and Fage (**13**, pp. 255–6). All the material used in our work has from the first been derived from the salt-marsh, Chelson Meadow, and any notes on the conditions in the wild refer to this place.

In later years, however, great changes have taken place in the ditches, in depth, temperature and salinity (**39**, p. 27). Little attention has been given to the drainage, the Meadow itself is under water at times before the sluice-gates are operated, and, on such occasions it becomes impossible to reach the ditches for dredging.

The Gammarus, too, have changed their habitat to the shallower ditches farther inland, and dredgings taken at different times show extraordinary fluctuations in the numbers of the population. They have changed also in that many different recessive factors have appeared in the stock. The eye-pigments do not appear to be as stable as heretofore, partial or complete absence of the white pigment occurs and reddening or decrease in the amount of the black pigment (p. 376) is also found. It seems to us that these changes may perhaps be related in some degree to the change in the conditions.

If, when the ditches are overflowing, the sluice-gates are opened, and a great volume of water pours out, it must carry with it most of the inhabitants of the ditches. Only a small nucleus would be left and therefore any recessive factors that were present would be multiplied by interbreeding, and rapidly conveyed through the whole of the Stock to reappear again and again. That this is what happens appears to us probable from the evidence obtained, e.g. the r_2 gene was found for the first time in the laboratory cultures in 1922 (p. 372), reappeared in 1930 (p. 380), again in 1931 (p. 387) and 1932 (p. 399), in numbers in 1933 (pp. 401, 402), and now in 1935 one Red-eyed specimen carrying the r_2 gene has been found in the natural conditions in the ditches (p. 402).

DESCRIPTION OF *GAMMARUS CHEVREUXI*.

Gammarus chevreuxi is a small species of amphipod, the largest male recorded measuring 14·5 mm., and the largest female 9 mm. from the tip of the rostrum along the dorsum to the tip of the telson. The body is laterally compressed and semi-transparent with the internal organs showing through the thin chitinous cuticle. In the normal wild type the pigmentation of the body is pale green, yellow-green in the males, bluer green in the females with bands of brown on the antennæ. The gonads and eggs in the female are dark green, almost black. The sessile eyes are compound* and well developed, reniform in shape with the margin entire and clearly defined, lightly convex, the corneal cuticle smooth and not faceted. Each eye or ommateum is composed of a number of ommatidia arranged in regular rows, the numbers increasing on the periphery at the growth-stages, and rising from 10–12 in the newly hatched to 70 or 80 in the adult. Each ommatidium has an oval lens formed of two crystalline cones, with the rhabdome, immediately below the cones, surrounded by 5 retinular cells, 4 large and 1 small, containing the coloured pigment. The interstices between the ommatidia are filled with the large so-called "accessory-pigment cells" carrying the opaque chalk-white pigment; seen from above, this has the aspect of a superficial raised white reticulation spread over the eye-surface, with the ommatidia showing as round coloured spots deep in the meshes of the network.

The granular retinal pigment in the normal wild eye when first laid down in the embryo is a pure bright Red, which darkens rather rapidly through Intermediate Red and Dark Red to jet-Black just before extrusion from the egg-capsule.

Two pigments are involved, of different origin and constitution. The black is permanent, and insoluble in any of the preservatives tried. The red is soluble in alcohol, and fades completely out after a time, whilst the white interommatidial pigment is evanescent, and instantly soluble in water or any of the other liquids used. It disintegrates as soon as death takes place, and rises in irregular masses to the surface of the eye, thence to disappear within a few hours. In any disturbance of the eye involving the different pigments, such as the "Clotted-eye" (**48**, p. 695), it has been noted that the granular retinal pigment sinks, while the white pigment rises to the surface.

Moulting and Development (**12** and **21**).

The development of Gammarus after leaving the egg may be described as a series of growth-stages each terminated by a moult, or casting of the hard chitinous cuticle. The period between moults is short in the immature, and the increase in size and change in proportions considerable at each stage up to the time of sexual maturity. "The difference in the *proportion* the various parts of the body bear to each other is very marked, e.g. the head in the newly hatched young is much larger in proportion, about a seventh of the total length of the body measured dorsally, and the peræon and pleon are practically equal in length, whilst in the mature animal the head is an eleventh of the total length, and the peræon is a third as long again as the pleon" (**12**, p. 365).

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* For a description of the structure see G. H. Parker, The Compound Eye in Crustaceans. Bull. Mus. Comp. Zool. Harvard, XXI, No. 2, 1891.

The *rate* of development is affected to a great degree by temperature. In summer the time taken to reach sexual maturity may be from 34 to 40 days, in winter from 2 to 4 months, but the characters are not affected in any way by the difference in rate.

The development of the young *Gammarus chevreuxi* takes place in a series of seven growth-stages before sexual maturity is reached. The sexes are indistinguishable by any external character up to the fifth stage; they are identical in size, proportions and even to the exact number of setæ and spines. Even at the fifth stage they are still almost indistinguishable, for though minute broodplates are present in the female, it needs a high power to see them. At the sixth stage the differentiation of the secondary sexual characters becomes more evident, the broodplates are larger, and one or two curved hairs of the peculiar male type appear on the male's lower antennæ, but it is not until the next stage, the seventh, that the sexual difference can be seen with the naked eye. Pairing generally takes place during this period, but no mating is possible until after the moult. In the next stage, the eighth, the eggs are laid and fertilised. The female's development is now practically finished, but the male undergoes two further stages and great modification of the secondary characters before it reaches its definitive adult form (**12**, p. 385).

At this period (Stage 8) the animals although sexually mature have only reached about half their growth. From then onwards until they attain the maximum length of the species they moult at longer intervals, and the increase in size, though constant, is much more gradual and therefore less noticeable at each stage. After full growth is established the difference between the stages is hardly perceptible; a few more setæ may appear, the colour darken, or the chitin become thicker.

For a further discussion of this section, see Appendix I, page 407.

The Question of Telegony.

As soon as the first mutant, the Red-eye, appeared in the 1912 Stock, and before any mendelian experiments were started, the question as to possible telegony in the species had to be settled. The structure and breeding-habits of *G. chevreuxi*, the species chosen for the work, were therefore studied, and compared with six other species of the genus Gammarus. The conclusion reached was "that it is absolutely impossible for a male to fertilise two broods of eggs with one deposition of sperm" (**3**, p. 19).

Briefly stated, the facts for *G. chevreuxi* are as follows:—

(*a*) the female never lays eggs in the absence of a male; (even in those species, e.g. *G. locusta* and *G. duebeni*, where batches of eggs are sometimes laid without a male present, the eggs are always infertile and are thrown off within a very short time) ;

(*b*) the animals never pair until the female is in the right physiological condition ;

(*c*) once paired, they remain together, the male carrying the female till mating is accomplished ;

(*d*) mating is always preceded by the female's moult ;

(*e*) in moulting, the old cuticle cracks across behind the cephalon, on the dorsal surface, and the female draws herself out backwards through this dorsal opening leaving the ventral surface unbroken, so that the old brood pouch (which is attached ventrally to the 2nd, 3rd, 4th and 5th pairs of legs) is sloughed off as a whole ;

(*f*) fertilisation takes place externally,* the male ejecting the sperm into the open new pouch before the eggs are extruded ;

(*g*) the eggs are laid into the pouch, where they develop ;

(*h*) during the whole period of incubation of the eggs the pleopods drive a steady current of water through the pouch from behind forwards ;

(*i*) and, finally, the young when hatched do not emerge for at least 24 hours, but keep in constant movement in the pouch feeding on anything that may be washed in through the openings at either end (**45**, p. 477).

This seemed sufficient proof that the sperm from one mating could not be carried over to the next, but other tests were devised to make assurance sure.

If it were possible that sperm could remain in the pouch and active through one reproductive period to the next (and it must be remembered that these periods last sometimes for three months in the winter), then an ovigerous female kept by herself should be capable of laying a second and fertile batch of eggs in the absence of the male. Numbers of females were therefore taken at different seasons of the year, and mated, and then, after the eggs were laid, the males were removed from the brood-bowls, and the females kept separate for one, two, or more breeding periods, sometimes up to six months. Never once were eggs laid in the absence of a male : but all these females, when mated again later on, gave the expected results with their new mates.

A number of cross matings were also made (Red female mated first with a Black male and then with a Red one), but in these, as well as in all the cross matings that have since been made from 1912 till now, we have never had a single instance of a male influencing any offspring subsequent to his own.

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* Le Roux makes the same observation with reference to another Gammarus species, *G. duebeni* (**37**, p. 31). " On se rend compte sur coupes, que la plus grande partie des spermatozöides se trouve dans la poche incubatrice, autour des orifices genitaux et *qu'ils ne pénètrent pas dans les oviductes*."

MUTANT CHARACTERS AS THEY APPEARED IN THE LABORATORY CULTURES.

Gammarus chevreuxi has proved an exceptionally good material for a study of the nature of the variations in structure or in physiological processes. So far, the experimental data on this question can be sorted into three distinct groups, though others may appear later.

I. First, there are the variations which are inherited in a strictly mendelian fashion and which are evidently the result of the presence of recessive genes. They may be classed as follows as affecting

a. the pigmentation of the body, e.g. *White-body* (**16**, pp. 194–195);

b. the structure of the eye, e.g. the *Albino* (**41**, p. 274);

c. the coloured retinal pigments, e.g. *Red-eye*: *White-eye* (**16**, p. 194), *Lilac* (**38**, p. 201), etc.;

d. the white interommatidial pigment, e.g. *Nowhite* (**3**, p. 43);

e. both the coloured retinal and the white interommatidial pigments, such as the *Nowhite-Red* (**38**, p. 201).

II. Secondly, there are the variations which appear more or less to affect all the members of certain stocks, where the line of demarcation is not so much between normal and aberrant as between the degrees of intensity of the abnormality. The precise genetical interpretation of the transmission of the variations has not yet been elucidated. Such are

a. *Gradual Nowhite*, with reduction of the white pigment;

b. *Gradual Normal*, with increase of the White pigment;

c. *Irregular Coloured-eye*, with its furthest manifestations, the *One-eyed*, and *No-eyes*,

d. and the *Clotted-eye* (**48**, pp. 692–695).

III. The third group consists of those variations which have not been proved to have a direct connection with "genes," but which, because they occur in some stocks, often in succeeding generations, and not at all in others, must have an hereditary basis of some sort. Such, for example, are :—

a. *Spottedness*, i.e. presence of spots of white pigment, apart from the eye, on the head and first peræon segment;

b. *Half-Nowhite*, in which one eye has the normal white reticulation and the other eye none;

c. *Non-mendelian Nowhites*, which arise sporadically in certain stocks;

d. *Variations* in the intensity or amount of the coloured pigments.

THE 1912 EXPERIMENT.

Stock I.

The first mutation arose in 1912 in the F_2 from a black eyed pair brought in from Chelson Meadow. Nine of the first brood of the pair came to maturity, three males and six females, and were mated *inter se* and with outside mates. All gave black-eyed offspring with one exception, a female. She was mated first in her own brood with male A and hatched two broods, in each of which one red-eyed appeared among the black. She was then tested with a male from a freshly brought in dredging and gave 40 Black- and 4 Red-eyed young; put back again with male A, she had another brood, 39 Black and 3 Red. Both the males, and the other animals in the cultures and in the fresh dredging were tested for Red, and matings were carried out for several generations but no Reds appeared, only normal Black-eyed young were hatched.

The Red was tested and proved recessive in the simple mendelian ratio 3 : 1. In one experiment, where the F_2 broods were examined for eye colour as they hatched, out of 1004 young, 251 were Red-eyed. It is now known as **Stock 1 Red** (r_1 gene).

All our stock in the laboratory, together with what we have distributed to colleges and teaching institutions, has been derived from the third brood of this one female. The mutation has never again arisen from the wild.

The colour, a full bright clear red, is very stable through life and has not varied in the pure Main Stock I in all the years since its first appearance, though it was noted (**6**, p. 348) that in very old animals the red colour tended to darken with age. It has not been affected by the temperatures at which we keep our cultures, but that darkening can be induced by constant high temperature (23° C.) has been shown by Ford and Huxley (**20**, p. 115, and **26**, p. 68).

Other mutant characters which arose later in this Stock I were connected with the structure of the eye, and it is noteworthy that these, like the Red r_1 gene, only occurred once and have never appeared again.

The second departure from the normal was the **Albino*** (**4**, p. 274), a sharply defined and heritable mutation, which behaves as a simple mendelian recessive. In this form, the whole structure of the eye is degenerate, the ommateum is broken up, the retinular cells are lacking and only a few scattered cones and interommatidial cells remain. The white pigment forms irregular curd-like masses in the eye, and spots, streaks or splashes of white, apart from the eye, on the cephalon and first

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* For a discussion of the structure of the Albino eye see Wolsky and Huxley (**42**); and particularly Wolsky (**49**).

peræon-segment. The "spotted" condition appears to be closely connected with instability of eye-structure, the spots appearing in certain definite positions (**6**, p. 353).

The third variation, again a case of defective eye-structure, the **Irregular Coloured** eye (**33**, pp. 355–393), arose in the offspring of a mating between one of the dorsally spotted Albinos and a Black Nowhite male heterozygous for Red; i.e. on the one side brought in by the male: the normal regularity of shape and structure in the ommateum and individual ommatidia, the presence of the retinular cells containing the coloured pigment, the presence of the interommatidial cells, but absence of white pigment; and, on the other side by the female: the ommateum degenerate and broken, no retinular cells present, the interommatidial cells present and scattered and greatly reduced in number, but containing white pigment and the white pigment also in spots on the head.

The range of variation in the succeeding generations was extraordinarily wide, extending at birth from the typical normal-eye—perfect in shape and pigmentation—through all stages of degeneracy to the complete loss of one or of both eyes. The extreme stages of degeneracy, the **One-eyed**, and the **No-eyes** or Blind forms, were usually associated with malformation of the head and brain. **Intersexuality** in varying degree (**7**, pp. 549–550: and **12**, pp. 388–396), and other abnormalities in the reproductive organs were frequent throughout this stock.

The line of inheritance could not be clearly defined, owing to the gradual onset of the irregularity, even animals born "normal-eyed" becoming affected later, and to its tendency to increase in intensity throughout life, as well as to the high mortality in the young stages especially amongst those born "abnormal-eyed." It is interesting to trace the series of degenerative stages in a perfectly normal-eyed race which ended in the loss of one or of both eyes, and the rate at which it was accomplished—only eight years. The first Black-eyed pair was brought in from the wild in June, 1912; the first Red-eyed arose in the F_2 generation in August, 1912; the Albino appeared from heterozygous parents in June, 1915; the Nowhite later also from heterozygous parents; the mating referred to above, heterozygous Black Nowhite × Albino was made in 1918; and the first completely Blind form appeared in the F_3 in May, 1920.

All these genetic variations in our stock were produced in laboratory cultures, and had never been encountered in the wild. But, in a very striking example of eye-degeneration, recently recorded in the case of another amphipod, the same amount of variation can be parallelled in a wild population and in a much greater frequency.

The authors, Gallien and David (1936, **50**, pp. 184–196) have described collections of the common sandhopper, *Talitrus saltator* Montagu, brought in from the wild, in which the range of mutant characters extended from Red-eye to the loss of one eye, and included practically every departure from the normal known in *G. chevreuxi*. To gain an idea of the frequency of the occurrence and the proportion of normal to un-normal, a collection of 700 Talitrus was examined; 3 were "spotted" "taches cephaliques blanches" and 30 were found with "malformations oculaires," but if the lesser cases, such as occasional depigmented ommatidia, had been included, it would have worked out at 8% not strictly normal.

Another genetic variation in Stock I was the **Nowhite** which affected the interommatidial white "accessory pigment," completely inhibiting its appearance. This also proved to be a mendelian recessive, with the 3 : 1 ratio. It is now known as the *Genotypic Nowhite* to distinguish it from the other Nowhite types which developed later, such as, e.g. *Phenotypic* (**48**, p. 692). The genotypic Nowhites hatch nowhite, and remain so throughout life; they give nowhite young when mated *inter se* or with other genotypic nowhite stocks; and an F_2 ratio of 3 : 1 when mated with normals.

The phenotypic nowhites are indistinguishable in appearance from the genotypic. They also hatch nowhite and remain so through life, but they give normal-eyed young when mated with other phenotypic nowhites, or with the genotypic; and normals or normals and nowhites when mated *inter se*.

The Nowhite variation is not peculiar to this Stock, but has been found in many strains and even in the wild. Throughout the records we have used the letter "**N**" to denote the Nowhite type, as, e.g. **BN**. for Black Nowhite; **RN**., Red Nowhite; **AN**., Albino Nowhite or "Colourless" as we first named it from its lack of both the white and the coloured pigments (**4**, pp. 330–339). Later, after the appearance of the White-eye, and its White-Nowhite form, **WN**., to which the description would equally apply, "colourless" as a term was dropped. The letters **HN**. for Half, or One-sided Nowhites, are used to distinguish those animals in which one eye has the interommatidial white pigment present, and the other eye has none.

THE 1922 TEMPERATURE EXPERIMENT.

During the ten years from 1912 to 1922 dredgings were taken at frequent intervals and cultures carried on in the laboratory to the F_2 and F_3 generations, but nothing occurred out of the normal, the retinal colour was always black, the white reticulation was present and "spots" were exceedingly rare.

In 1922, however, it became plain that heterozygosity must exist in what we had hitherto regarded as a homogeneous population, new factors appearing in several of the stocks derived from a dredging brought in on Sept. 12th. The animals were intended mainly for use in studying the influence of temperature on development and reproduction. The young were not examined for eye colour until red-eyes were seen in the F_2 offspring of one of the Incubator pairs. A short résumé of the results may be given here.

Temperature and Rate of Development.

Ninety-five mated pairs were taken, all with eggs laid on the same date, so as to start on the same level. They were divided into five series, three at temperatures as nearly uniform as possible, viz.: extreme heat, medium, and extreme cold: and two in varying temperatures, viz.: indoors in laboratory conditions, and outdoors in natural conditions. Daily observations were made with maximum and minimum thermometers (Negretti and Zambra).

Table I shows the highest reading of the maximum thermometer, and the lowest reading of the minimum for the month, and the average of daily readings taken at 10 a.m. through the month, for four Series.

Series I. Uniform High Temperature.

For this, an incubator was used, kept as nearly as possible to 20°–21° C.

The results were as follows:—

F_1 broods took on the average 10 days in winter (Nov., Dec., and Jan.), from oviposition to the extrusion of the young from the brood-pouch; 8 to 9 days from April to October.

Age of the first F_1 pair to mate and lay eggs was 145 days.

F_2. Eggs laid.	Eggs hatched.	
Mar. 1.	Mar. 5.	Thrown off.
Mar. 6.	Mar. 10.	Thrown off.
Mar. 16.	Mar. 25.	Young (3) extruded.
Mar. 25.	Mar. 31.	Thrown off.
April 4.	April 13.	Young extruded.

and 16 broods since.

F_3. Nearly mature in June.

Series II. Varying Indoor Conditions in a compartment on the north side of the laboratory.

This series was subject to considerable variations of temperature, daily as well as seasonal. The highest summer temperature in the period was 22° C. on June 30, and the lowest winter reading was 8·3° C. on December 11. The daily range occasionally varied in the 24 hours by 2 to as much

TABLE I.

1922 TEMPERATURE EXPERIMENT.

Date of record.	Maximum temperature for the month. °C	Date of record.	Minimum temperature for the month. °C.	Month.	Average temperature for the month. °C.
Series I : Incubator.					
1922.					
Sept. 21	22·6 °C	Sept. 27	20·5 °C	Sept. 16–30	21·5 °C
Oct. 2	22·2	Oct. 31	18·0	Oct.	20·93
Nov. 13	22·0	Nov. 22	17·5	Nov.	20·15
Dec. 25	21·0	Dec. 25	17·0	Dec.	19·57
1923.		1923.		1923.	
Jan. 16, 19	21·0	Jan. 1, 6, 12	17·5	Jan.	19·77
Feb. 15	21·4	Feb. 23	17·8	Feb.	19·8
March 26	21·9	March 24	17·8	March	20·12
April 30	22·4	April 14	17·2	April	20·0
May 31	22·7	May 14	18·0	May	20·0
June 25	25·2	June 11	19·6	June	21·4
Series II : Varying Indoor Conditions.					
1922.				1922.	
Sept. 28	20·0	Sept. 30	13·0	Sept. 16–30	15·3
Oct. 13	19·3	Oct. 30	9·0	Oct.	13·0
Nov. 11	18·9	Nov. 27	10·0	Nov.	13·8
Dec. 2	16·0	Dec. 11	8·3	Dec.	12·8
1923.		1923.		1923.	
Jan. 31	17·0	Jan. 13	9·3	Jan.	12·3
Feb. 2	19·5	Feb. 23	10·0	Feb.	14·5
March 9, 26	18·0	March 5	11·3	March	14·69
April 30	18·0	April 10	8·9	April	13·76
May 5, 22	20·0	May 11, 12	10·6	May	16·0
June 30	22·0	June 20	13·0	June	16·93
Series III : Uniform Moderate Temperature.					
1922.				1922.	
Sept. 25	15·3	Sept. 16, 18	13·5	Sept. 16–30	14·3
Oct. 2	14·8	Oct. 30, 31	10·0	Oct.	12·45
Nov. 11	12·3	Nov. 1, 6	10·0	Nov.	10·74
Dec. 2, 6, 7, 14, 15, 16	11·2	Dec. 28, 29	9·5	Dec.	10·3
1923.		1923.		1923.	
Jan. 4	10·1	Jan. 13, 15, 22	8·3	Jan.	8·94
Feb. 5	11·2	Feb. 24	8·9	Feb.	9·97
March 28, 29	11·8	March 12	9·3	March	9·96
April 4	11·4	April 10, 11	9·3	April	10·25
May 5	13·1	May 1	10·5	May	11·43
June 28	15·3	June 1	11·8	June	13·22
Series IV : Varying Outdoor Conditions.					
1922.					
Sept. 21	18·4	Sept. 18	8·3	Sept. 16–30	12·55
Oct. 14	16·9	Oct. 30, 31	2·5	Oct.	9·08
Nov. 11	13·0	Nov. 14, 27	−0·5	Nov.	7·22
Dec. 14	11·4	Dec. 11	−1·0	Dec.	7·17
1923.		1923.		1923.	
Jan. 31	11·0	Jan. 13	−0·2	Jan.	6·03
Feb. 1	10·9	Feb. 20	1·9	Feb.	7·75
March 26	15·6	March 5	1·8	March	7·75
April 3	16·0	April 28	2·9	April	8·97
May 4	20·9	May 12	3·1	May	9·78
June 30	22·0	June 5	8·9	June	13·56

as 6 degrees Centigrade. F_1 broods took 15–20 days to hatch from October to January; 12–14 days in the warmer months.

Age of the first pair to mate, at the time of oviposition, was 121 days.

F_2. Eggs laid.	Eggs hatched.
Feb. 12.	Mar. 1. Young (2) extruded.
Mar. 2.	Mar. 17. Young (6) extruded and ♀ eaten.

It is noteworthy that the F_1 of this series, matured *earlier* than the Incubator F_1, 121 days as compared with 145, and that the first batch of eggs hatched and the young F_2 were extruded on the same day that the first batch of eggs was laid in the Incubator.

Series III. Uniform moderate temperature.

The desired conditions were found in the experimental tanks on the north side of the laboratory, which are fed from an underground reservoir, and kept in constant circulation. The temperature was practically steady during the different months, and though it varied with the season, there were no sudden rises and falls as in Series II and IV. The daily range was about 1 degree Centigrade. F_1 broods took on the average 23–30 days to hatch, from November to April; and 16–18 days in June and July.

Age of the first pair to mate, at time of oviposition, was 157 days.

F_2. Eggs laid.	Eggs hatched.
May 2	Thrown off.
May 22	June 12. Young extruded.

The male and female of this pair were hatched on November 26, 1922, but matured earlier than the second pair, which were hatched on November 22. These were 167 days old when their first batch of eggs was laid on May 8; and the young were extruded on May 30.

Series IV. Varying Outdoor Conditions.

The jars were kept on the flat roof of the laboratory in a large weighted packing-case, so that although exposed to the air, they were protected from the force of the wind and from the direct rays of the sun.

The temperature varied from $-1°$ C. in winter to 22° C. in June. The daily range in April was roughly 6–7° C.

F_1 broods took 35–48 days from November to April and 15–20 days from April to June.

The first F_1 pair to mate and lay eggs was 176 days old.

F_2. Eggs laid June 6. Young extruded June 26. The second pair was 191 days old; eggs were laid on June 22; and the young hatched July 5.

Series V. Uniform extreme cold.

Twenty-eight pairs were kept in separate finger-bowls in an ice-chest, all the females having laid eggs the day they were put in. The temperature was fairly steady at 2·5° to 3° C., but a rise of about a degree took place daily for a few minutes when the chest had to be opened for examining the bowls and adding fresh ice.

The females were well-grown, and their batches of eggs of the usual average number for their size, about 40 to a batch. It was found that not only was development greatly retarded by the cold which, of course, was to be expected, but that there was a very high mortality just at the hatching period; this had not been anticipated in view of the fact that broods had survived occasional much lower temperatures in the "varying conditions" experiment.

The results were as follows:—

Out of the 28 bowls, 11 females threw off their eggs within from 1 to 2 months, 8 of them dying at the same time. In 9 females, the eggs were thrown off gradually until only one or two were left in the batch. These were carried until orange (i.e. embryos fully formed, but still enclosed in the egg-capsules) for periods of 68, 71, 74, 75, 81, 84, 90, 94 and 96 days respectively, but none hatched.

In one case, where the eggs had been thrown off, and the male had died, a second male which had been the same time in the ice-chest, 80 days, was put in, mated immediately and a few eggs were laid in 5 days. These gradually disappeared until at 39 days 3 were left macerating.

Only 7 females hatched any young.

No. of Broods.	Hatched in Days.	No. of Young.	New Eggs Laid.
1 brood	71	3	Laid same day, carried 95 days.
1 ,,	72–75	7	Laid 19 days after extrusion.
1 ,,	74	1 and others dead in pouch.	
1 ,,	74	1 and 1 partly developed.	
1 ,,	77	4	1st batch; thrown off at 5 days; 2nd batch laid after 80 days; thrown off at 35 days; 3rd batch laid after 79 days; thrown off at 19 days.
1 ,,	85	4 dead.	Laid 2 days later.
1 ,,	98–99	3	Laid 2 days later and carried 75 days.

In all, 15 batches of eggs were laid in the ice-conditions, and carried in some cases for weeks, but not a single young one was hatched.

A comparison may be made of all the series : broods of eggs laid within a day or two of each other in the first week of November hatched as follows :—

In *Series I* in 9 days ; *II* in 15 days ; *III* in 22 days ; *IV* in 42 days ; and *V* in 77 and 85 days.

By February 26, 1923, the pairs in the different series had given :—

I, 13 broods and eggs not yet hatched.
II, 6 ,, ,, orange.
III, 5 ,, ,, not yet hatched.
IV, 3 ,, ,, ,, ,,
V, 1 brood, no eggs.

As soon as the work reached the F_2 generation it was seen that new recessive factors were present in several of the stocks, affecting the pigmentation of the body as well as of the eyes.

Three of these arose in the Incubator series, viz. two new Red-eye recessives, one in Stock II (r_2) and one in Stock IV (r_4). The third, " White-body " also in Stock II, was connected with the body-pigment. Two more Red-eyes appeared in the second series, " varying indoor conditions," one in Stock III (r_3), and one in the F_2 from another strain which unfortunately did not survive to be tested (2 specimens only, bright red, one normal-eyed and one Nowhite).

A slight reddening of the black pigment was noticed also in the offspring of three other pairs, at or near maturity, but this would appear to be of no significance genetically. It has been observed occasionally in animals freshly brought in as well as in laboratory cultures, but interbreeding with them has never produced anything but the ordinary normal black type.

STOCK II.

Stock II (**21**, p. 50 ; **28**, p. 191 ; **31**, p. 313) was of great interest and importance. It contained two new recessive factors, one for Red (r_2) affecting the pigmentation of the eye, and the other, the White-body, inhibiting the normal-coloured pigment of the body and red eye-colour.

The **Stock II Red** gene has reappeared many times in the course of the work, and is still present in the wild population.

On its first appearance in this, the " Main Stock," the colour was a vivid bright clear red, stable throughout the life of the individual, and through the succeeding generations.

But in later years, as new stocks appeared carrying this r_2 gene, a remarkable difference was noted and it was soon recognised that some modifying factor or factors must be present, affecting the deposition of the pigments, the coloured retinal and the interommatidial white.

We found that on taking all these stocks together they fell into two distinct classes, (*a*) *stable eye-colour*, and (*b*) *unstable eye-colour*.

Class a. The "Main Stock II" is the type of Class *a*, *Stable Eye-colour*, in which the full bright red of the eyes on hatching remains unchanged through life. It has remained stable in our cultures whether the animals are reared in the incubator heat or in the cooler laboratory conditions.

Included in this division are :—

Main Stock II.	Incubator, inside mating,	p. 372
MM. LXIX.	,, ,, ,,	p. 390
K. XXXV.	Laboratory, outside,	p. 399
dd. XXXIX.	Incubator, inside,	p. 402 ; **54**, p. 355
dd. XLIII.	,, ,,	p. ,, ,, ,,
dd. LXX.	,, ,,	p. ,, ,, ,,
dd. LXXIII.	,, ,,	p. ,, ,, ,,

Class b. *Unstable Eye-colour.* In this class, whilst the principal recessive gene is the same as in *a*, some modifying factors are evidently at work causing great fluctuation in the deposition of the pigments, and consequent variations in the intensity of the red coloration.

The range of colour in the retinular pigment is from pale cream or white (i.e. practically no pigment in the retinular cells) through all shades of rose-pink, pale red, orange, bright red and lilac to a dark ruby-red and reddish purple. It has been found impossible to draw a dividing line between the colour tones or to establish any of the shades as a "pure" line, for in many of the animals through life a definite increase or decrease in the amount of pigment deposited takes place. All the intermatings gave Reds, but the variations in the intensity and amount of pigment deposited in the parents' eyes were not necessarily heritable, e.g. Cream × Cream often gave bright full Reds.

The Stocks in this division are :—

S. XIV.	Incubator, inside mating	p. 381
S. XV.	,, ,, ,,	p. 381
M. XVI.	Laboratory ,, ,,	p. 387
M. XVI A.	,, outside	p. 387
M. XL.	,, inside mating	p. 388
M. LII.	,, ,, ,,	p. 389
D. XXXI.	Natural conditions, inside mating	p. 401 ; **54**, p. 340
D. XXXI A.	,, ,, outside mating	p. ,, ,, p. 340
D. XLVI.	,, ,, inside mating	p. ,, ,, p. 341
D. LIII A. & *D. LIII.*	,, ,, outside and inside mating	p. ,, ,, p. 342
D. LXIV A. & *D. LXIV.*	,, ,, outside and inside mating	p. ,, ,, p. 342

The white accessory pigment, also, varied from the normal amount of white reticulation to none, i.e. Nowhite.

The other variation from the normal in Stock II was the "**White-body**," recessive to the pigmented form. In this is found a factor inhibiting the production of the carotinoid pigments, the green of the normal body, and the red of the eyes. The whole animal is pearly white, with not the slightest tinge of colour anywhere in the body, gonads or eggs.

This mutation arose at the same time as the new Red-eye (r_2) (**16**, p. 195), the brood in which they both occurred consisting of Black-eyed animals, some green-bodied, some white-bodied; Red-eyed, green-bodied; and White-eyed, white-bodied (i.e. Reds homozygous for "white-body" and therefore lacking the coloured pigment in body and eyes.)

The white body factor had a remarkable effect on the crosses between the normal form and the mutant. Different results were given according to the sex of the mutant employed; and a new type, the "Changeling," was produced.

For example, in all matings of White-body White-eyed male × Green-body Black-eyed female all the offspring were green-bodied and black-eyed; but the reciprocal cross Green-body Black-eyed male × White-body White-eyed female always gave black-eyed young which were *white-bodied* at birth, but which later developed the green body-pigment—the so-called "**Changeling Blacks**."

Again, in all the Red matings White-body White-eyed male × Green-body Red-eyed female gave all normal green-bodied red-eyed young; but the reciprocal cross Green-body Red-eyed male × White-body White-eyed female produced young, *white-bodied* and *white-eyed* at birth, which later developed pigment in body and eyes and became indistinguishable from the normal green-bodied red-eyed animals. These we called the "**Changeling Whites**."

The following explanation was suggested (**19**, pp. 119–120). Individuals homozygous for the white-body factor cannot lay down body-pigment or red eye-pigment, consequently white-body females lay eggs with no pigment. The developing embryo has therefore no pigment even if the fertilising sperm carries the colour factor. A White individual results which changes to Red as life proceeds, since the dominant normal colour factor introduced by the father is able later to make good the deficit of pigment.

It will be seen that Changeling Whites occur only where Reds would be expected; they always have a White-bodied mother, and always behave genetically as Reds, but are always heterozygous for White-body.

The White eyes are of different kinds. When they first arose in the F_2 they were of the **Flushed-white** type, i.e. eyes in which the ommatidia, quite white at birth, develop the faintest tinge of pink, only visible under a high power, by the time maturity is reached. These, the oldest ommatidia, form the centre of the eye, but the later ommatidia, which increase on the periphery at each growth-stage, remain white always. For a similar happening with coloured eyes see page 393.

The **Quite White** type segregated out in the F_7 generation and are still going. They breed true and have never developed the slightest trace of colour in the eyes or in any part of the body.

Another division of the Whites is known as the **Purple-whites**, from the purple colour which in varying degrees of intensity partially or completely covers the eye. The pigmentation apparently differs in constitution from the granular red and black contents of the retinular cells in the normal eye which retain their colour after dissection and even after preservation, the red for some considerable time, and the black permanently. In the Purple-whites, on the contrary, as soon as the ommatidia are exposed to the air after dissection the colour fades out completely with the greatest rapidity, although later, after some hours or days in the preservative, a faint dull grey tint appears looking like a thin sediment in the bottom of the eye. A chemical analysis has unfortunately not been possible, owing to scarcity of material.

The first Purple-whites appeared amongst the descendants of a cross made with a Flushed White female of this Stock mated to a Red male of Stock I.

They are of several different types, of which the most distinct are :—

Flushed Purple, a White-eye, with the central ommatidia tinged with dark or pale rosy lilac ;

Half Purple, in which the upper half of the eye is white, the lower part lilac-purple ;

Purple-white, in which the whole of the eye is flushed pale or dark purple ; and the

Blackberry-purple, with the pigment in quantity and almost purple-black in tone, the shade of a ripe blackberry.

The White-body mutation has only appeared twice—in this Stock heterozygous for Red and in the F_2 from a homozygous Black pair *M. XXIV* (p. 387) brought in from the wild in 1931. Mated together they proved to be the same genotypically.

It has been frequently noted throughout the work that crosses between the recessives of different strains produce great modifications, and consequent new colour-combinations. For example the cross just mentioned between Stocks I and II gave the new colour Purple-white. Again in the cross between Stocks I and III, the r_1r_1 types were quite distinct from the typical normal clear Reds of the Main Stock—they all showed a darkening in the centre of the eyes (**31**, p. 311). In the cross between Stocks I and V, to take another instance out of many, the r_1r_1 types are quite stable and fully pigmented in the Main Stock, but display in the cross great variation and deficiency of the red pigment (**31**, p. 321).

Stock III.

Stock III Red (**21**, p. 51 ; **31**, pp. 313–315) differed from the other Reds, r_1, r_2, and r_4, in that it arose gradually. Some of the Black F_1 became reddish, and mating *inter se* gave an F_2 containing Black, Reddish Black, Dark Red, Intermediate and Bright Reds, with a new departure "**Mosaic** Eye" in which some of the ommatidia were black and some bright red (see **33**, Plate III).

Stock IV.

Stock IV Reds (**16**, p. 195 ; **21**, p. 51 ; and, **31** pp. 315–319) were of different shades, Dark Red sometimes almost black, and Light Red. Dark Reds tended to lighten in colour, but always functioned as Dark Reds and gave Dark and Light offspring. Light Reds consisted of Bright Reds and others slightly deeper in tone ; they gave always Light Red offspring.

THE 1928 H. EXPERIMENT.

Meanwhile, dredgings were still being made in the ditches and thousands of animals examined yearly, but only very slight variations were noted, of little significance compared with the immense numbers of normal. For example, there was sometimes a reduction of the black retinal pigment (reddening) or of the white pigment of the eye (thin reticulation) or a slight increase in the number of the "spotted," but nothing of any importance until the spring of 1928.

During January and February of that year, dredgings were brought in for an incubator-experiment. The ditches were flooded, and overflowing their banks, and it was found that the Gammarus had changed their location and gone farther up the water-courses to the shallower parts. The February collection contained a large preponderance of males.

Thirty-nine pairs were set out at a temperature of 20·8° C., but the heat, gradually raised until it reached 28° C., proved too much for most of the animals. Only four stocks reached the F_3 generation.

"*Reddening*," in varying degree, was of comparatively frequent occurrence, but this, as has been said before, appears to have little or no genetical significance, and may simply be due to an increase in the rate of development, and a consequent inability to produce the black pigment in sufficient quantity to keep pace with growth. As would be expected, it occurs more frequently in the Incubator Stocks than in the laboratory cultures, but seems to have no effect on the offspring.

Only four stocks (three of which died out) gave Red-eyes (**28**, p. 199), viz.:

H. I, in which Reddish Blacks and 12 Intermediate Reds appeared in the F_3 and F_4 generations; only 1 Reddish Black in F_5.

H. VIII, with 13 Reddish Black, 8 Intermediate Red and 6 Bright Red in the F_2; only 3 Reddish Black in the F_3.

H. XXV, with 1 Red, dead at extrusion, in the F_2; and *H. XXXI*, known as Stock V, which proved one of the most difficult of all the stocks with which we have worked.

STOCK V.

Stock V Red (**28**, pp. 194–217; and **31**, pp. 319–335). The account given in the above references describes the experimental work on this stock as far as it had proceeded at the time of publication. It was stated that the conclusions then drawn from it might, and probably would, have to be modified if the results of later investigation should render it necessary and, in fact, certain alterations must be made as shown in the discussion below (see also p. 380).

On its first appearance the new stock was characterised by several striking features:—

1. An extraordinary variety of colour-changes and fluctuation in eye-colour in the individual animals, sometimes in one direction, either darkening or lightening, sometimes, but less often, changing from the one direction to the other and back again, at the growth-stages.

It has been shown that the retinal pigment is first laid down in the embryo (**21**, pp. 45–46) as bright clear red, some time before the black is deposited—the eye-colour changing as the deposit of dark pigment increases first to intermediate red, through dark red and finally to black on hatching. In the typical normal eye this deposit of black keeps pace with growth, masking the red, and the eye-colour is always a dense jet-black, but in the new Stock V the *rate* of the deposition of the two pigments, black and red, appears to fluctuate considerably, and so causes the colour to vary according to which pigment is produced in the greater quantity during any one growth-stage. As we have said before, "any alteration in this balance means a change in eye-coloration" (**28**, p. 216). For example, in the true "Blacks" group, a reduced rate in the deposition will give "dilute black," a thin greyish black tone or purplish black. In the "Reds" group the fluctuations and grades of colour show much more distinctly; with a larger amount of black the Reddish Blacks and Reddish Purples are produced; with a lesser admixture the Dark Reds and Intermediate Reds, whilst a form which we called "New Red" contains only the faintest trace of dark pigment, just enough to deepen the red tint in the eye. The difference between this colour and the normal bright red of Stocks I and II is very slight; but in preserved specimens, where the red pigment is dissolved out, the New Reds show a faint dark deposit, whilst the normal Reds are perfectly clear, and without the slightest trace of it. It must be noted that this extensive range of colour is produced by the admixture in different proportions of two pigments only, black and red.

2. Although the main facts of inheritance were clear (the simple mendelian ratio of 3 : 1), yet, owing to this fluctuation of colour in the recessives, the pigmentation of the parents' eyes was no indicator of the colour of the offsprings' eyes at birth, nor was the colour at any given period a reliable guide to later developments; a Black might lighten to Red, or an Intermediate Red darken to Reddish Black or to almost Black. Nor was it possible to separate the animals by the difference in the rate of pigment-deposition. The rate appeared to vary even in the individual, and instances frequently occurred in which more black than red would be developed at one growth-stage, and more red than black at the next.

3. No pure Bright Reds were known from the Main Stock up to the F_6 generation, at the time of the publication of the results. All the Reds which were produced in the earlier generations had some admixture of dark pigment, and this at first was considered to be a definite character of the new gene (r_5). Even the brightest, the "New Reds," as they were called, contained a trace of it, faint but distinct, though only perceptible to the naked eye as a slight deepening of colour, just a shade deeper than the normal pure bright red of Stocks I and II.

Meanwhile, from a cross (*OH. 745*) which had been made between an F_4 recessive male of the Main Stock, and a Black "Outside" female from the wild, the pure Red had segregated out in the F_2 free from the slightest trace of dark pigment.

It was at first thought that a new gene had made its appearance, and as such it was recorded and named r_6, but the evidence was not considered sufficiently conclusive, and the experimental work was therefore carried further. The later investigation has now definitely proved its identity with the r_5 gene.

These Pure Reds were mated with typical "Stock V Reds" of the same *Cross OH. 745*; and back to Main Stock V recessives; and later with another Stock *MM. XV A.* (a reappearance of r_5), and gave reds, and reds only, with them all (p. 379).

That this deduction was correct as to the identity with r_5 has since been confirmed by the appearance of the Pure Reds in the Main Stock itself, in the F_7 generation. And to put the matter beyond question it was found when a specimen was preserved in alcohol and the red pigment dissolved out that there was no trace of any deposit of dark pigment; the eyes were perfectly colourless.

The history of the *Cross OH. 745* in which the pure normal Red segregated out was as follows :—

A male, *H. 745*, of Main Stock V (F_2 of a pair which gave Blacks, Reddish Blacks and Intermediate almost bright Reds) was mated with a Black female freshly brought in from the wild. The male was a recessive, with eyes which looked Black on hatching, but which gradually reddened until, at the time of mating, they were Red to the naked eye; two months after the second brood of the cross was hatched, they developed a purplish tone, and eventually became pale Reddish Purple.

The two broods of the cross consisted of 17 Black (1 spotted) (*OH. 850*) and 30 Black (*OH. 856*). Eleven of the 47 survived to breed, 3 males and 3 females of the first brood, of which 2 males and 1 female had become Reddish Black by maturity; and 2 males and 3 females of the second brood.

Their intermatings gave an F_2 of 200 Black* (37 spotted) and 126 Reds (19 spotted), which included 31 Reddish Blacks, 2 Dark Reds, 30 Intermediate Reds of all grades from dark to almost bright red, and 33 of the pure normal Reds.

The following matings were made :

Mixed matings in the brood-bowls : gave 25 B. (2 spd.); 9 RB. (2 spd.); and 1 Int. Red.

B♂$_1$×B♀$_1$ *850* : 32 B. (5 spd.); 8 RB.; and 9 Int. Red (2 spd.).

B♂$_1$×B♀$_3$ *850* : 22 B. (4 spd.); 1 RB.; and 11 Int. Red.

B♀$_1$×B♂ of *856* : 36 B. (6 spd.); 8 RB. (1 spd.); and 16 Int. Red (3 spd.).

B♂$_2$×B♀$_2$ of *850* which had both become Reddish Black, gave 85 B. (20 spd.); 5 RB. (2 spd.); 2 Dark Red; 23 Int. Red (6 spd.); and 33 pure normal Reds (5 spd.).

These "pure Reds" were tested in several ways, first to make sure of their identity with Stock V, and then to prove the distinction of Stock V from the other tested stock reds, such as Stock I and Stock II Reds, and Stock *LVII*, Nowhite Red. From the numerous matings made, the following examples are taken to illustrate the results :—

Ex. 1. *Test Cross 2070.* Mating of a pure Red with a typical Stock V Red, both from the *Cross OH. 745.*

Pure Red ♀ *OH. 2046*×Dark Reddish Purple ♂ *OH. 2070* gave an F_1

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* The figures given for the Blacks and Reddish-blacks refer only to the colour at birth and cannot be regarded as giving the correct constitution of the animals. All these young were hatched in the incubator, and it is known that in this Stock, the dark pigment is deposited in greater amount in the higher temperature. The survivors were too few to be of any use in checking the figures.

brood of 15 Light Int. Red, and an F_2 of 1 Dark Red; 1 Light Int. Red; and 1 Pure Red.

Ex. 2. *MC. LXV.* The same ♂ *OH. 2070* of Ex. 1 was mated back to a typical "Stock V red," an Int. Red→Red ♀, F_4 *MM XV A.* (p. 391; Table II) and gave in the F_1, 12 Dark Red, two of them Half-Nowhite; in the F_2 6 Dark Red; and in the F_3* 2 Reddish Black and 2 Dark Red.

Ex. 3. *OH. 1506 b.* 2. Mating of a Pure Red ♂ with a typical "Stock V red" from the same stock. *Cross OH. 745.*

Pure Red ♂ *OH. 1549 c.*×Dark Reddish Purple ♀ *OH. 1506* gave 66 Red offspring, of which 16 were Pure Reds and the others typical Stock V reds with all their characteristics, fluctuation of colour, etc. The same range of colour was repeated in the F_3 and F_4 generations. Intermatings of the F_2 Pure Normal Reds produced, as would be expected, all Pure Normal Reds.

Ex. 4. *Test Cross 1549 c.* The same ♂ *OH. 1549 c.* of Ex. 3 was mated back to a Main Stock V recessive, Int. Red. → almost-Red ♀, *H. 1507* and gave 3 broods of 3 Light Int. Red; 3 rather darker Int. Red; and 3 very light Intermediate Reds. The 7 survivors all lightened to the same tint, an almost-Red. Intermatings gave an F_2 of 116 of which 21 were recorded as "Pure Red" at birth. The other 95 ranged from Dark Intermediate to bright, almost Red, but the colour gradations were so close to each other that it was almost impossible to draw a line between them. Two broods examined within a few hours of hatching gave the proportions as 21 Int. Red; 12 New Red; and 4 Pure Normal Red. The same variety of colours reappeared in the F_3 and F_4 generations.

These Pure Normal Reds crossed with the Reds of other Stocks, e.g. Stock I Red Nowhite; Stock II Red; and Stock *LVII* Nowhite-Red (p. 397) gave all Blacks, the different Reds segregating out in the F_2 in the usual mendelian ratio.

THE 1930 S. EXPERIMENT.

The second statement requiring correction is the association of the "Flesh Red-eye" with a new gene *f* (**31**, p. 335). Later investigation has proved this to be yet another manifestation of the r_2 gene, the "unstable eye-colour" type (p. 373).

The specimens came from a small dredging brought in November, 1930, and kept by Mr. Spooner in the incubator (**32**, published May, 1932). Thirteen pairs were bred from, with recessives appearing in the F_2 generation of three of them:—

In *S. XVI*, the Nowhite variation occurred, and was found to be genotypically the same as the Nowhite of Stock I.

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* Found mature, not examined on hatching.

In *S. XIV*, two recessive forms were described, Flesh Red (gene *f*) and Beet Red (gene *t*), segregating independently of Flesh. Flesh is given as varying from normal Red to almost colourless: and Beet as having red eyes at extrusion but with "an appreciable amount of dark pigment which gives it the appearance of New, Intermediate or Dark Red. During the earlier growth-stages the eye darkens rapidly to a Reddish Black or even Black, the final state varying among individuals."

In *S. XV* also Flesh Reds appeared (F_2, 47 Blacks and 6 Flesh) which when mated with the Flesh Reds of *S. XIV* proved identical.

The Flesh-reds had been tested with Stock I Red and shown to be distinct from it (see also **31**, p. 312, where mention is made of the cross). We know now that Flesh is really Stock II Red, "unstable" division, and that the varying tones of colour compare with other stocks carrying the r_2 recessive.

Other crosses have been made since then, establishing beyond question the identity of the Flesh gene *f* with the r_2 gene of Stock II.

Some of the crosses made were as under :—

Exp. 1. *MC. LIV.* Flesh ♂×Quite White ♀ *TH. 6064* gave 10 Changelings (1 spd.). These intermated, producing Reds and Whites in the next generation.

Exp. 2 *dd. 681.* One of the F_2 Reds of Exp. 1, a ♀, mated with a Red ♂ *dd. 681* (F_3 *dd. LXXIII*) and gave two broods numbering 28 Reds, all with full red colour when mature.

Exp. 3. *MC. XLV.* Flesh ♀×Red ♂ (F_3 *MM. LXIX*) gave 32 Reds (5 spd.).

Exp. 4. Flesh ♂ of the bright red type×Nowhite-Red ♀, F_4 Stock *LVII* gave 5 Black (2 spd.).

THE 1931 M. EXPERIMENT.

In 1931 we decided to make as large an experiment as could be conveniently handled to try and get a conclusive ruling on the question of heterozygosity in the wild—as to whether it was inherent in the stock (which seemed certain from the previous evidence), or was caused by the abnormal conditions to which it was subjected in the laboratory, such as extremes of temperature, changes of salinity, depth, food, etc.

For this purpose a dredging was brought in on October 6, 1931, which, in many ways, proved by far the most interesting of any we have ever had. Unfortunately, some bacterial infection was introduced during the later work, probably through the water, which wiped out some stocks, and reduced others to such an extent that we realised that the figures obtained from the work could hardly be called conclusive.

It was evident that another experiment must be instituted to complete

TABLE

1931 M. EXPERIMENT :

FROM OUTSIDE MATING OF ♀.

	F_1	F_2		
Stock No.	Black.	Black.	Red.	
M. I A.	3	57		1 survivor→almost BN.=♀
M. II A.	8	287		3 reddish tinge
M. III A.	8	166		11 reddish tinge (2→B.)
M. IV A.	13	118		F_1 13 dilute ; F_2 16 reddish tinge
M. V A.	10	401		3 reddish tinge
M. VI A.	18	159		
M. VIII A.	3	21		
M. IX A.	8	64		2 reddish tinge
M. XI A.	18	108 & 1 BN.*		*Nowhites* in F_2 and F_3
M. XV A.	38	45		**Red-eye** in F_3
M. XVI A.	20	261	**38.**	**Red-eye** in F_2 (=reappearance of the r_2 gene)
M. XVIII A.	24	238		In brood of 6, 1* Dark Red→RB.→jet B.
M. XXIII A.	14	—		
M. XXIV A.	14	33		Some reddish tinge.
M. XXVIII A.	7	43		
M. XL A.	23	2		
M. LII A.	17	2		

II.

LABORATORY CONDITIONS.

FROM INSIDE MATING OF ♀.

	F_1		F_2				
Stock No.	Black.	Survivors.	Black.	BN.	HN.	Red.	
M. I	101	41	431	3*			*Gradual Nowhite* in F_2 and F_3.
M. II	125	75	746				1 almost Nowhite→B. normal.
M. III	124	62	537	18	9		1 BN. and 2 HN. spotted and irreg. *Phenotypic Nowhite* in F_2.
M. IV	32	6	16				
M. V	92 B. : 1 BN.	51 B : 1 BN	300	1	1 and 17		Clotted-eyes. F_1 1 BN.*; F_2 some reddish; variation in white pigment; irregularity; new mutation in F_2, **Clotted-eye.**
M. VI	126	74	275				F_1, 1 sl. reddish ♂.
M. VIII	17	11	242				Deficiency of white pigment in many.
M. IX	87	34	436	5	2		Irregularity in 1 BN. and 1 HN.; deficiency of white pigment in many; many Gradual Nowhites; *Phenotypic Nowhites* in F_2 and F_3.
M. XI	—		—				
M. XV	106	9	94				No Reds appeared; an F_3 of 60 Black which died before they could be tested.
M. XVI	195	22	810	—	—	**97.**	324 B. and 94 R. were from hetero B. matings; **Red-eye** in F_2 ($=r_2$).
M. XVIII	126	3	—				
M. XXIII	125	25	125	—	1	—	
M. XXIV	125	13	182				Many of them Whitebody (about 3 : 1 ratio). **White-body** in F_2 (reappearance of genotype).
M. XXVIII	156 & 2* HN.	39	563				F_1 2 HN.*
M. XL	120	5	13	—	—	**2.**	Deficiency of white pigment. **Red-eye** in F_2 (= reappearance of r_2 gene).
M. LII	137	4	4	—	—	**1.**	**Red-eye** in F_2 (= reappearance of r_2 gene); in crosses with St. II Nowhites appeared, and great variation in the white pigment.

TABLE

1931 M. EXPERIMENT:

FROM OUTSIDE MATING OF ♀.

Stock No.	F_1 Black.	Colour variation at maturity.	F_2 Black.	RB.	BN.	HN.	Red.
MM. I A.	8		–				
MM. III A.	18	15 survivors, all reddish tinge	322	–	–	1	–
MM. VI A.	7		–				
MM. X A.	13		177				
MM. XV A.	11	4 reddish tinge	119	–	–	–	3 **Int. R. Red-eye** in F_2 (= reappearance of r_5 gene)
MM. XVII A.	21		129				
MM. XX A.	18	3 reddish tinge	677	–	1	5	66 **Lilac,** new recessive type in F_2; great variation in white pigment.
MM. XXIII A.	20	1 reddish tinge	151	–	–	–	
MM. XXVII A.	20	10 reddish tinge (and 1 with thin retic. also)	53	1*	–	1	–
MM. XXIX A.	22		14	–	–	1	–
MM. XXXI A.	18	1 reddish tinge	69	–	–	–	–
MM. XXXII A.	15		25	–	1	–	–
MM. XXXIX A.	21	2 reddish tinge	65	–	–	1	–
MM. XL A.	19		57	4*	1	1	–
MM. XLV A.	17	5 reddish and 1→RB.	67				
MM. XLVI A.	23	18 = 6 reddish and 12→RB.	96	4*	–	–	–
MM. L A.	11	10, all reddish tinge	162	–	–	–	–
MM. LVII A.	12	1 irregular	49	–	–	–	12 **Nowhite-Red**: new recessive type in F_2.
MM. LXII A.	14	All reddish tinge	–				
MM. LXVII A.	14	All reddish, 1→RB.	42				6 Dark Red and 1 **Int. Red. Red-eye** in F_2 not proved
MM. LXVIII A.	16		3				1 **Red, HN. Red-eye** in F_2 not proved
MM. LXIX A.	17	Dilute pigment	–				

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* Not examined at birth and therefore not to be accepted as

III.

INCUBATOR CONDITIONS.

FROM INSIDE MATING OF ♀.

	F$_1$				F$_2$				
Stock No.	Black.	BN.	HN.	Colour variation.	Black.	RB.	BN.	Red.	
MM. I	47	1 (sp.)	2	31 sl. reddish	158	1*			7 with sl. reddish tinge ; 7 thin retic.
MM. III	37	–	–	23 sl. reddish ; 1 thin retic.	330	–	1	-	
MM. VI	50	–	–	1 sl. reddish	110				
MM. X	39			All sl. reddish ; 7 thin retic.	82	–	1		4 sl. reddish.
MM. XV	12	–	–	10 sl. reddish	17	–	–	-	
MM. XVII	2	–	–		-				
MM. XX	38	1 (sp.)	2	and 1 irregular	36	–	–	–	No Lilac.
	-	–	–						
MM. XXVII	10	–	–		29	–		-	
MM. XXIX	12			5 sl. reddish	–				
MM. XXXI	8			All sl. reddish	37	–	-		7 sl. reddish.
MM. XXXII	7			4 sl. reddish	7	–			
	–								
	–								
MM. L	41	–	1	3→almost BN.	216	11*			1→RB., and 1 very thin retic.
MM. LVII	75			1 irreg., 1→thin retic. and 1 sl. reddish	102				2 ♀♀→sl. reddish and gave **Nowhite-Red** in F$_3$.
MM. LXII	4				73	–	2	–	4 thin retic.
MM. LXVII	8				5	–	–	-	
MM. LXVIII	–								
MM. LXIX	11				355	–	–	**15.**	**Red-eye** in F$_2$ (given by one pair, 42 : 15) = reappearance of r_2 gene.

the " birth-colour." All the RB. mated gave Black offspring.

the proof (p. 400), and we have set out the results of this experiment in Tables II and III and the paper which precedes this summary (**54**, pp. 319–356); except for a letter to *Nature* (**38**, pp. 201–202) recording the appearance of certain new recessives, none of the detail of this work has been published till now.

Details of the M. Experiment. Dredgings were taken on October 6 and 19, 1931, and 280 animals were set out, 70 pairs in the heat, and 70 pairs in laboratory conditions. They were all black-eyed, many with a slight reddish tinge, or dilute pigment, and many more with the white reticulation noticeably thin (see p. 398). From the October 19 dredging, for example, 25 out of the 38 pairs set out in laboratory conditions had thin reticulation, both males and females.

The mated pairs which were taken for the work, were those of which the females were ovigerous, i.e. females which had mated previously in the wild and laid eggs fertilised by other mates before pairing with their present mates. These broods, when extruded, were kept for comparison with the broods from the new matings, as we wished to ascertain if any distinction would appear between the young from eggs laid in the wild, and hatched indoors (the "*Outside*" mating), and the young from eggs laid, as well as hatched, indoors (the "*Inside*" mating). This was the first time that such a comparison had been made, but as will be seen in the above table, no distinction could be drawn between them.

The results obtained were unexpected. The highest number of variations, nine, appeared in the offspring from the Inside mating, laboratory conditions, and the lowest number, one, in the Inside mating, Incubator conditions.

The details are:—

LABORATORY CONDITIONS, *Outside* mating, three variations, viz. in the F_2, 1 Red-eye, a reappearance of the r_2 gene; 1 Nowhite, apparently genotypic: in the F_3, 1 Red-eye new ?. *Inside* mating F_2, 3 Red-eyes, reappearances of the r_2 gene; 1 reappearance of White-body; 1 new mutation, the Clotted-eye; and 4 Nowhites, one the Gradual Nowhite, two Phenotypic, and one not proved which appeared only in the crosses made with the stock.

INCUBATOR CONDITIONS, *Outside* mating, five variations, viz. 3 Red-eyes, 1 a reappearance of the r_5 gene, 2 not proved; 2 new mutations, the Nowhite-Red, and the Lilac-eye. *Inside* mating, only one, a Red-eye, a reappearance of the r_2 gene.

The variations fall into three classes, viz.: I. Changes in body-colour; II. Changes in the retinal colour of the eyes; and III. Changes in the white pigment of the eyes.

I. CHANGES IN BODY-COLOUR.

The White-body recessive reappeared in Stock *XXIV* (Inside laboratory) and was proved, by crossing, to be genetically the same as that in Stock II (p. 374).

In the F_1, 125 Black were hatched, but only 13 survived to maturity, and of these one brood alone (*M. 307*) gave healthy offspring.

An F_2 of 182 was produced, divided roughly into green-body Black-eyed, and white-body Black-eyed in the proportion of 3 : 1. Unfortunately, exact figures cannot be given for the body-colours at birth, owing to the difficulty of distinguishing them in the semi-transparent, 1 mm.-long young, and to the great mortality amongst them. The demarcation was clear in the older ones, and as many matings as possible were made, both in the stock, and with Main Stock II White-body.

To give one example: a white-bodied, Black-eyed female (*M. 537 b.*) was mated with a green-bodied male of her own stock, and gave 44 Changeling Blacks, i.e. white-bodied at birth, but developing the full green colour later: next with a white-bodied male of her own stock and gave two broods, 51 white-bodied young: and finally, mated with a Quite White male of Stock II (white-bodied, white-eyed), she had a brood of 19 white-bodied young.

II. CHANGES IN THE RETINAL EYE-COLOUR.

a. Reappearance of the r_2 gene.

The reappearance of the r_2 gene of the Stock II red-eye occurred in no less than 5 of the new stocks, viz.: *M. XVI A., XVI, XL, LII* and *MM. LXIX*.

M. XVI A, Outside, laboratory, and *M. XVI*, Inside, laboratory, may be considered together, their constitution being the same. The Red-eye factor in both was evidently brought in by the female parent, and appeared in the F_2 generation in the simple mendelian ratio 3 : 1. The male parent, *M. XVI*, was tested with two F_2 Red females (giving 24 Black with one, and 9 Black with the other) and proved to be homozygous for Black.

These stocks belong to the (*b*) class of Stock II Red, "unstable eye-colour" (p. 373) and show the great variation in the colour of the red-eye, with a range from cream, through all shades of primrose, rose-pink, pale red, bright red, cherry-red, to dark red and purplish. The fluctuation in colour in some individuals was very marked, cream on hatching developing to full red, and others beginning as red and fading to cream. That these practically White-eyed animals were true Reds was known by their matings, their offspring being hatched bright full red.

An example may be given: a female, hatched bright red, but with the colour fading, was mated with the parent male and gave 9 Black young: then she was put with a Red male, also paling. In both the colour faded to almost white, with only the faintest tinge of pink in two or three ommatidia, exactly like a Flushed White (except that the body was very dark green). They mated, and had a brood of 18 bright Red-eyes. These young, later, also paled.

The *M. XVI A.* brood consisted of 20 Black young of which 19 survived, 2 males and 17 females. Owing to the scarcity of males, it was not possible to test all the females conclusively, but the constitution of 10 animals was definitely proved. Five homozygous, 1 male and 4 females, and 5 heterozygous, 1 male and 4 females.

The homozygous male was mated with 9 females (two known to be homozygous and one heterozygous), and gave an F_2 of 73 Blacks.

The heterozygous male was put with 8 females, and gave an F_2—in mixed broods, 44 Black and 7 bright Red; with 2 heterozygous females (one gave 17 B., 3 R. and the other 33 B. and 19 R.; and a brood between them of 10 B., 4 R.), a total of 60 Black and 26 Reds; with a third heterozygous female, 16 Black and 5 Red; and with two proved homozygous females, 16 Black and 18 Black respectively. The total for the F_2 generation was 261 Blacks to 38 Reds.

Crosses were made between *XVI* and *XVI A.* to prove their identity, and in addition they were tested nine times with stocks carrying the r_2 gene, viz.: 2 matings with Main *Stock II*, 1 with *M. XL*, 1 with *M. LII*, 1 with *MM. LXIX* (stable eye-colour), 1 with *dd. LXXIII*, 2 with *D. LIII* and 1 with *K. XXXV A.* All the shades of Red were tried in these matings, and in every case the young were hatched bright red (193 in all). Two matings with heterozygous Black are given under *M. LII.* Six crosses were made with other mutant Stock Reds, 1 with Stock I Red, 2 with *MMB. LVII* Nowhite-Red and 3 with *M. XV A.*, one being Primrose × Primrose, and gave all Blacks (151).

M. XL. Inside mating, in varying laboratory conditions. This was a very small stock, carrying the r_2 gene, (*b*) division of Stock II, unstable eye-colour.

Only 5 F_1 survived out of 120 hatched. They gave two broods, 7 Black, and 6 Black and 2 Red pale in colour.

One of the latter reached maturity, a male, and was used for testing. It was first tried with a Red female from *MM. LXIX* of the (*a*) division, stable eye-colour; 25 young were hatched with bright red eyes, which *remained unchanged;* then with a Nowhite-Red female, Stock *LVII*, with which it had Black-eyed young. By that time its eyes had faded to almost White, so it was mated with a female of the same type (i.e. Red→Flushed White) from *M. XVI A.*, and gave 24 young with bright Red eyes.

Only one pair of the Blacks of the same brood had offspring, viz.: 3 broods of 6 Black, 5 of them very spotted, and 3 Half-Nowhite also; 4 Black, all spotted, and 2 of them Half-Nowhite; and 6 Black, 2 spotted. This result was interesting as showing that the white pigment as well as the coloured was affected in this mutating stock. Eleven out of the 16 animals were very spotted, in 5 of these the eye on one side was Nowhite, and in each case the Left eye.

M. LII. Inside mating, in varying laboratory conditions—another small stock belonging to the (*b*) division Stock II Red.

The Black-eyed F_1 numbered 137, but only the last brood survived and intermated in the brood-bowl. One F_2 brood was produced, of which 3 Black males, 1 Black female and 1 Pale Red male came to maturity. Matings in the bowl gave one F_3 brood, consisting of 5 Black and 2 Dark Primrose, i.e. Reds with so little colour that only the faintest tinge of primrose could be seen in the centres of the eyes. These two died without offspring, but one F_4 brood was given by the Blacks, viz. 2 Jet-black and 1 Dark Red—and with these the main stock came to an end.

Three males, 2 Black and the Pale Red, were left of the F_2 and crosses were made with these to prove the identity of this stock with Stock II.

The Pale Red male was tested with four different females:

MC. I. First with a female from *M. XVI A*, known to carry the r_2 factor, with eyes the same dilute shade of red; the young produced numbered 33, all with full bright red pigment.

MC. II. with a Red female from *MM. LXIX* (the (*a*) division, stable colour); offspring 13 bright Red.

MC. XII. with a Quite White female of Main Stock II; 89 Changeling Whites were hatched, 86 normal-eyed (13 spotted), 1 White-Nowhite spotted, and 2 White Half-Nowhites spotted; and finally with a Nowhite-Red female of the *LVII* Stock. This mating produced 42 Black young (4 spotted).

One of the surviving F_2 Black males was mated with a Red female from the *XVI A.* strain (r_2), and gave 58 Blacks and 64 Reds in four broods. The difference in the colour of the Reds on hatching was noticeable.

In the first brood, 2 Red were hatched, rather pale red. They matured, male and female, and gave a brood of 10 young with pale pink eyes, much paler than the parents.

The second brood consisted of 9 Reds, of a full clear colour. These came to maturity with the bright red pigment unchanged.

The third brood gave 19 Reds, of which 8 survived. In them all the colour had faded almost completely, leaving only a faint orange shade in the centres, like the Flushed White type.

In the fourth brood 34 Reds were hatched all pale in colour, but none survived.

The second surviving F_2 Black male was crossed with a Red female of *M. XVI* (r_2 factor), in which the colour faded gradually until the eyes became almost white with only a pinkish-purple flush in the centres. Four broods were produced consisting of 73 Black (11 spotted) and 61 Red (13 spotted).

In the 9 Reds of the first brood the colour lessened as they grew; the 19 Reds (12 spd.) of the second brood were hatched full clear red and remained unchanged; the 18 (1 spd.) of the third brood were Dark Primrose at birth, but the colour increased to pale red; and in the fourth the 15 were hatched pale pink, unspotted.

The second brood of this cross gave unusual figures, showing a great variation in the white pigment from Spots, "excess," to Nowhite, its complete absence. The numbers at birth were: as to coloured pigment, 15 Black to 19 Red; as to presence of white pigment in the normal white reticulation, to complete or partial absence, 25 : 9; and as to Spotted compared with unspotted, 20 : 14. They were divided as follows: 12 Black normal-eyed (5 spotted); 1 spotted BN.; 1 spotted Black HN. with irregular Nowhite right eye; 1 spotted Black, with the right eye almost Nowhite; 13 bright Red normal-eyed (6 spd.); 4 spotted RN., two also irregular-eyed; and 2 spotted Red HN. Unfortunately none survived to breed, and no information could be obtained as to inheritance.

It is known that the deposition of the white pigment is totally inhibited in the Genotypic Nowhites, but these Spotted Nowhites would appear to be in a different category. Judging from external evidence only, it looks as if the white pigment might have been deposited in normal quantity and released or set free from the cells in which it was formed, by some tension or pressure of the covering cuticle. We know that the white pigment, unlike the coloured granular retinular pigment, is fluid and flows easily together (cf. Clotted-eye, p. 399) into "spots" or "curd-like masses"; and that these spots frequently change position and shape at the moults; that they are found apart from the eye in certain definite positions (**6**, p. 353); and that the spots on the Spotted One-sided Nowhites are always very large on the nowhite side.

MM. LXIX. Inside mating, Incubator conditions. Only one F_1 brood was produced in the "Inside" stock of which eleven came to maturity, seven males and four females. Ten matings were made using different males and females, the offspring totalling 355 Black and 15 Red; 42 Black and the 15 Red came from one pair.

The Red was tested and found to belong to the (*a*) division of Stock II Reds, normal stable bright red colour. This type has persisted all through the generations, and is still to be seen in the F_8.

Crosses have been made with four other stocks carrying the r_2 factor, viz. *M. LII*, *M. XVI A.*, *M. XL* and the "*Flesh-red*," with all of which Red-eyed offspring were produced. Tested with Reds from Stock V (r_5) and *MM. XV A.* (r_5); *M. XV A.*; *MM. XX A.* the "Lilac" Stock; and *MM. LVII A.* Nowhite-Red, Black-eyed young were given in each case.

b. Reappearance of the r_5 gene.

The reappearance of the r_5 gene, showing the same wide range of colour and fluctuation of colour in the individual, as in Stock V, occurred as follows :—

MM. XV A. Incubator conditions, "Outside" mating of ♀ *MM. XV.* The brood consisted of 11 Black, of which 10 survived to maturity, 7 males and 3 females.

The 3 females were paired, with the following results :—

Pair 1 had 3 broods of 8 Black; 1 Black, slight reddish tinge; and a brood not examined till six weeks old when 7 survivors were found, 4 Black and 3 Dark Intermediate Reds. Only 3 of the first brood survived to maturity; Black male and female, and Black male →Reddish Purple →Int. Red. This male was mated with a Black female from the *Pair 2* mating. They had 44 Black offspring which, mated *inter se*, gave in the F_3 97 Black, 5 Deep Red and 17 Intermediate Red. Ten of these 17 became mature, with changes of eye-colour from Red to Dark Reddish Purple; bred together, their offspring numbered 54, viz. 4 Reddish Purple, 13 Intermediate Red and 37 Light Int. Red. One of the females an Int. Red→Red was mated with a Stock II Red and a Stock V Dark Reddish Purple; with the first male she had 38 Black young, and with the second she gave 12 Dark Red (2 HN. spotted).

Pair 2 gave 80 Black in 8 broods—the female was then tried with the heterozygous male of *Pair 1*, and proved homozygous, giving 20 Blacks. Presumably male *2* was also homozygous, the 47 F_3 offspring of chance matings in the bowl, and the 35 F_4 were all Black-eyed.

Pair 3 had no offspring.

c. Description of Three other Red-eyes.

Three other Red-eyes which appeared in this experiment will now be described. Unfortunately the numbers were small and could not be sufficiently tested.

Details are as follows :—

M. XV A. Laboratory conditions, from the female's Outside mating.

The brood numbered 38 Black, but very few came to maturity. Interbreeding in the bowl gave an F_2 of 45 Blacks (in very small broods, 3 : 1 : 3 : 2 : 4 : 3 : 6 : 17 ; and 6). Three animals reached maturity in the seventh brood, 2 males and 1 female, all heterozygous Black ; mated together an F_3 was produced of 79 Black (17 spd.) and 22 Red (3 spd.) (with one male, 27 B. (2 spd.)) and 2 Red ; with the second male 36 B. (11 spd.) and 14 Red (3 spd.) ; and "mixed," not known which male, 16 B. (4 spd.) and 6 Red.

Of the 22 Red F_3, 15 were bright red at birth and 7 pale red, but in all the colour lightened to a greater or less degree, e.g. in 4 of the bright Reds the eyes became almost White with only 2 or 3 flushed purple ommatidia in the centres. Of the Pale Reds, 1 lightened and 4 others remained unchanged. All died without offspring, except two "Pale Reds" which mated and gave 7 Pale Red young.

The change in the intensity of colour was reminiscent of Stock II, but crosses made with this stock and also with Stock V showed that neither the r_2 nor the r_5 gene was present.

Eleven crosses were made : one with a Quite White female of *Stock II* gave 24 Black Changelings ; three with *M. XVI* (r_2), Pale Red × Pale Red, and Primrose × Primrose, gave all Black ; as also did two crosses with *MM. LXIX* (r_2) and one with *Stock V* Red (r_5). A cross with *Stock I* failed.

The Inside mating of the female *M. XV* produced 106 in the F_1, but only 4 of these had any offspring, all Black. One F_1 male was crossed with a Red female *M. XVI A.* (r_2) and gave 32 Black (5 spd.) ; and one F_2 female was tried with a heterozygous F_2 male of *M. XV A.* and gave 20 Black (6 spd). No others survived to mate.

MM. LXVII A. Incubator conditions, "Outside" mating. Of the 16 Black of the brood, 14 survived, 6 males and 8 females. In none of these at maturity was the eye-colour of the normal jet-black intensity—4, 2 males and 2 females, showed a reddish tinge, one male more so than the others.

42 Blacks and 7 Reds were produced in the F_2 generation. The Reds consisted of 1 Intermediate Red, from chance matings in the bowl containing the 2 "reddish" Black males ; and 6 Dark Red in a brood of 18 given by a Black pair.

This was unfortunately one of those mutating stocks which die out rapidly owing to the difficulties in breeding them, either through feebleness, e.g. the Int. Red which became a female, but did not survive to mate, or through infertility, e.g. a Black female which mated and had eggs eight times, but hatched none ; or through cannibalism.

It was impossible to test the Reds, for only two survived, both females.

In one, the Inter. Red, the colour darkened slightly with growth, but not as far as the "dark red" shade. In the other, the only survivor of the 6 Dark Reds, an interesting development was noticed in the eye-colour. The Dark Red tone of the central and oldest ommatidia persisted, but all the later ommatidia as they formed on the periphery at the growth-stages were a clear pale orange-red, with no trace of the dark pigment. When preserved the orange-red dissolved out, leaving those ommatidia colourless, but the central ones showed a dark deposit.

This female was mated with a Nowhite-Red of Stock *LVII*, and was eaten by her mate after extruding a brood of 7 Black.

MM. LXVIII. Incubator conditions, Outside mating. This is another of the unsatisfactory small stocks referred to above.

The F_1 brood consisted of 16 Black-eyed, but the matings in the brood-bowls produced only 2 F_2 broods, 2 Black; and 2 Black and 1 Red Half-Nowhite.

Three survived, Black male and female, and the Red, a female. The male mated with the Black female, and had 30 Black young; and with the Red female, 3 Black. None of the young lived to maturity.

d. Appearance of Two New Mutant Characters.

There also appeared two quite new recessive types, the **Lilac**-eye, Stock *XX*, and the **Nowhite-Red**, Stock *LVII* (**38**, p. 27).

Stock XX. Lilac.

The Lilac mutation arose in the Incubator conditions from the "Outside" mating of female *MM. XX* and evidently derived from the Outside male parent. The female herself was homozygous for Black, as shown by the fact that only Black-eyed were produced in the four generations resulting from her mating with the male *XX* ("Inside" mating).

F_1 generation.

The brood of 18 normal Black-eyed young hatched on October 10, 1931, five days after being placed in the incubator. Sixteen survived, 7 males and 9 females. Mated together as far as it was possible, to test them, 1 ♂ and 1 ♀ (*Pair 6*) proved heterozygous for the new mutation Lilac-eye.

The results of the matings are as follows :—

	F_2		F_3		F_4	
Pair No.	Black.	Lilac.	Black.	Lilac.	Black.	Lilac.
Pair 1	36	—	14	—	—	—
Pair 2 hetero ♂ 6, ♀ 2	14	—	76	4	113	23
Pair 3	10	—	—	—	—	—
Pair 4	11 (1 BN.)	—	30 (1 HN.)	—	—	—
Pair 5	130 (1 HN.)	—	87 (1 BN.)	—	51	—
Pair 6 hetero ♂, ♀	190	66	189 (1 BN., 1 HN.)	170 (5 LN.)	104	56
Pair 7	5	—	—	—	—	—
Pair 8, ♂ 3, ♀ 7	38	—	9	—	3	—
Pair 10, ♂ 10, hetero ♀ 6	20	—	—	—	—	—
Pair 11, ♂ 5, ♀ 3	19	—	—	—	—	—
Pair 12=hetero ♂ 6, ♀ 5	120 (2 HN.)	—	—	—	—	—
Pair 13, ♂ 10, ♀ 5	23	—	—	—	—	—
Mixed Matings	61 (2 HN. sp.)	—	98 (1 HN., 1 irreg.)	—	23	—

This stock was an exceedingly difficult one to work with: the individual broods were usually of small numbers, many of the young died before maturity, and matings among the survivors were frequently infertile even with the normal-eyed animals. With regard to this infertility, a curious occurrence was noted in later generations (F_3 and F_4). Females, sometimes of the same brood, all with the normal body- and eye-colour, and gonads of the usual blackish green tone, gave different coloured eggs. Some laid the normal dark green fertile eggs, while others had their pouches full of opaque *white eggs*, very noticeable in life, the pearly whiteness of the egg mass showing up in startling contrast with the green body colour. Altogether 26 batches of white eggs were produced, but no young were ever hatched.

The details are as follows:—

In the F_2 one B. ♀→BN. gave 1 batch of white-eggs.

One F_2 pair (♂ 20×♀ 4·2) mated 7 times, five times with no results and twice with white-eggs.

A second F_2 pair (♂ 20×♀ 20) had 4 normal broods, but in the next generation one F_3 pair gave 6 white-egg broods.

A third F_2 pair (♂ 20·2×♀ 4·1) had 4 broods of normal eggs, but the white-eggs appeared in the next generation: one F_3 ♀ mated with 3 different males of her own brood, with one she had 7 broods of white-eggs, with the other two males she mated and separated without eggs. In another F_3 mating, two females and one male were left in the bowls, and 10 batches of white-eggs were laid.

Instability of the white pigment was another characteristic of the stock, ranging from excess of pigment, such as heavy reticulation and "spotting" to the deficiency or absence shown in partial or complete Nowhites.

In the F_2, besides the cases of "thin reticulation," 6 instances were found, 1 complete Black Nowhite, and 5 Half-Nowhites (2 spotted). The BN. became a female, and, mated with a Black male of its own brood, gave 29 Black and 1 Half-Nowhite; none survived. None of the HN. lived to maturity, but from the *Pair 5* brood in which the HN. appeared, 1 BN. was produced in the F_3, and 2 more BN. in the F_5. These, a male and female, had 4 offspring, which, when examined about a month after birth, were found to be 3 BN. with rather dilute pigment and 1 Black almost Nowhite, but with flecks of white reticulation.

From this result it would appear that the Nowhite is not the genotypic, but belongs to the class which we have named "phenotypic Nowhite" (see p. 367).

The instability of the white pigment was very marked in the Lilacs; in the later generations the white was sometimes lacking altogether, sometimes present only as streaks or flecks instead of the normal even reticulation.

The **Lilac-eyes**. The first of these appeared in the second, third and fourth broods of *Pair 6* and were on hatching a pale clear lilac colour with heavy white reticulation. The female parent was tried with another male for about six weeks, and then put back with male 6. In the broods following it was noted that the clear definite lilac tint of the three previous broods had changed or intensified in some way and that the tone on hatching was now more reddish and more clouded, an indefinable shade which we called "**Reddish Lilac**." This, however, was not the permanent condition as was soon made manifest in both the coloured and the white pigments, and to illustrate the full extent of the change and the rapidity with which it was accomplished, an instance may be taken from the development of the Lilacs in the seventh brood.

In three weeks after hatching the white reticulation had vanished, and the coloured pigment had cleared from the centres of the ommatidia and risen to form as a dense rim round the circumference of each, so that the eye looked like rings of dark pigment enclosing circles of a warm cream colour. It had the remarkable appearance of a dark brownish black reticulation on a light ground, instead of the usual white reticulation on a dark ground. This is the typical "**Creamy Lilac**" form, found in all the F_2 survivors.

Further changes in the Lilac colour were observed in the F_3 generation. The eyes of the F_3 young at birth looked exactly the same shade of lilac as those of the newly hatched F_2, but as they grew a difference soon became evident. The two forms, Reddish and Creamy, instead of merging one into the other, segregated out sharply into two distinct types, one, the *Creamy Lilac* as described above, and the other a *Reddish Lilac* in which the lilac colour remains in the retinular cells but develops and retains a much redder tone. The white reticulation in this type is not completely lost, usually some flecks or streaks of white persist, especially towards the periphery of the eye.

The **Lilac Nowhites**, also, first arose in the F_3. They are quite distinct from, and darker in colour than the Lilacs, a very dark plum colour, so concentrated as to look almost Black.

Details of the matings in the different colour groups will be found in Appendix II, p. 409.

STOCK LVII. NOWHITE-REDS.

This is another remarkable stock and the only one of the type found in the whole course of the work. In it, the recessive, Nowhite-Red, has the two mutant characters—red pigment instead of black, and no white-pigment instead of the normal white reticulation—always combined, and never segregating out one from the other.

The Red is a vivid bright cherry red, with all the retinular cells densely pigmented. It is distinct from the Reds of all our other stocks, and the Nowhite too is different. It seems that the factor which inhibits the appearance of the white only operates when combined with the *red* of this mutation. Mated with the genotypic Nowhites of other stocks, the normal white reticulation appears in the young. We have called this the "**Nowhite-Red**" to distinguish it from the other types of Nowhite.

The Stock arose from the "Outside" mating of the female *LVII.* The eggs were orange when brought in and were extruded next day in the incubator—12 Black-eyed young being produced.

Five survived to maturity, 2 males and 3 females, but only two can be said to have been thoroughly tested, the male and female of *Pair 1*—which gave 33 Blacks and 9 Nowhite-Reds. *Pair 2* had only 4 Black young; and the third female mated with male 1, had one brood of 8 Black. A brood was found just extruded by female 1 in the brood bowl before the pairs were separated, 4 Black and 3 Nowhite-Reds.

As will be seen, the Blacks and Nowhite-Reds appeared in the 3 : 1 ratio, and this has been maintained through the generations till now, when the F_6 are maturing.

Of the 49 Black and 12 Nowhite-Red in the F_2, only 13 survived to mate; 2 males and 8 females of the Black, and 1 male and 2 females of the Nowhite-Reds.

The results of the F_2 matings were as follows :—

Black×*Black*	Pair 1.	47 B.
	Pair 2.	9 B, 3 NR.
	Pair 4.	13 B, 7 NR.
and Mixed matings		21 B.
		48 B, 5 NR.
Nowhite Red×*Nowhite-Red*		94 NR.

The survivors of the 138 Black, 9 males and 13 females, and of the 109 Nowhite-Reds, 37 males and 33 females, produced a large F_3, the colours appearing according to expectation in the offspring.

Eighteen crosses were made between the Nowhite-Reds of this and the following generations, and the Reds and Red Nowhites of other stocks, viz. 3 with stocks carrying the r_1 gene ; 9 with others carrying the r_2 gene ; 2 with Stock V Intermediate Red, and Bright Red (39 young) ; 1 with a Red Nowhite male from a cross $r_1 \times r_5$ (22 young) ; 2 with the Lilac-eye ; and 1 with the Dark Red of *MM. LXVII A.* (7 young). The Nowhite-Red was proved to be definitely distinct from them all ; the offspring without exception were normal-eyed, with black pigment in the retinular cells and the white accessory pigment in an even reticulation over the eyes. The mortality was very high, and most of them died without breeding, but the results in those which reached the F_2 were as follows :—

With stock carrying the r_1 gene ; 3 crosses of Red Nowhite males of Stock I with Nowhite-Red females of *LVII* gave 30 normal-eyed Black young. The only survivor, a male (*M.C. 548*), was first mated back to a Main stock *LVII* Nowhite-Red female, and gave an F_1 of 24 Black ; 25 R.B. ; and[*] 47 Red nowhites.

Two matings of the F_1 *Blacks* gave 12 B., 3 RN. ; and 14 B., 3 RN. respectively. Matings of the *RB* gave 5 B., 1 Red ; 29 B., 3 RN. ; 22 B., 4 Red, 8 RN. ; and 6 B. *RN* by *RN* mixed matings were 22 RN. and 1 Red almost HN. ; 7 RN. ; and 13 RN. ; whilst two matings of *B*×*RN*, and *RN*×*B*, gave 43 B., 25 Red, 31 RN. ; and 25 B., 16 RN., respectively.

The same male *M.C. 548* was then crossed back to a Stock I Red Nowhite female, and produced an F_1 of 9 B. ; 3 BN. ; 5 Red ; and 6 RN.

With stocks carrying the r_2 gene ; 9 crosses, including two with Main Stock II white-body white-eggs, one cross with *XL*, one with *LII*, one with *S. XIV*, two with *LXIX*, one with *XVI A*, and one with *XVI*. In all, 249 black-eyed young were produced. The 13 offspring of the last cross (with *XVI*) mated *inter se* gave 50 B. ; 22 Red ; and 23 RN.

With the Lilac Stock ; 2 crosses, one of which with three matings gave only 4 young, all normal-eyed Black, and all spotted. Of these a male and two females reached maturity and gave in 4 broods, 8 Black, 2 Dark Red, and 4 Red nowhites (from one female, 4 B., 1 DR.; and 1 B., 3 RN.: from the other 1 B.; and 2 B. (1 spd.), 1 DR., and 1 RN.).

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[*] It is impossible to distinguish at birth between the Red Nowhites of the two stocks.

III. Changes in the Interommatidial White Pigment.

At the time of the commencement of the Gammarus work, the eye-pigments, coloured and white, were characterised by stability and only very rarely was anything noted as out of the normal. In 1928 (H. expt.) this statement no longer held good, and by 1931, the date of the M. experiment, the character of the wild population had completely changed in this respect. There was much instability, and reduction of the pigments throughout the stock, particularly in the interommatidial white. More animals were found with thin reticulation (i.e. with the white lines so faint and thread-like as to appear almost nowhite) than with the normal amount in the eyes.

In fact all the variations, genetic and non-genetic, that have yet appeared in the distribution of the white accessory pigment were seen in this experiment, some for the first time. The range was from *excess* of the white, "heavy reticulation" to *deficiency* of the pigment, "thin reticulation"; and from the evenly spaced distinct white reticulation, the *normal*, to its complete absence, the *Nowhite*. (See Table II, *M. VIII*, *IX*, *XL* and *MM. XX*, *A.*)

The *Gradual Nowhite* appeared in several stocks with its characteristic feature of the steady reduction of the white pigment to its complete loss, a "Nowhite" form indistinguishable at sight from the genotypic Nowhite, but functioning as a normal (**48**, p. 693). An example may be given from *M I* stock—an F_2 BN. ♂ of this type mated with a B. normal ♀ which had gradually lost nearly all the white pigment. The offspring produced were 5 Black, normal reticulation; 5 Black, very thin retic.; and 2 BN. When they were examined two months later, it was found that of the 5 B., "very thin retic.," three had become completely Nowhite, one almost nowhite, and one half-nowhite; whilst the "2 BN." had developed flecks of white.

To another variation, apparent for the first time in the work, we have given the name of "*Phenotypic*" Nowhite, in distinction from the "Genotypic." The two forms cannot be separated by appearance either at birth, or at any period of their lives, but the white factor is present in the one, the phenotypic, and absent in the other, the genotypic, and consequently when mated together, only normal-eyed young are produced.

The Nowhite of the Nowhite-Reds, *Stock LVII* (where the black and the white pigments are both inhibited) is also phenotypic.

Examples may also be seen in *M. III*; *M. IX*; *MM. XX A.* and others. In *M. III*, out of an F_2 of 564, 18 were phenotypic BN. (one spotted and irregular) and 9 HN. (two spotted and irregular). A mating BN×BN gave 8 BN. Another of BN×HN produced 22 Black; 6 BN.; and 1 HN. One of the BN., a female, was tested with a genotypic BN. male, and gave Black normal-eyes.

In the F_2 of *M. IX*, there were 5 phenotypic BN. (one irregular) and 2 HN. (one irregular). From a mating BN×BN, 7 BN. were hatched; and one of the BN. tested with a genotypic nowhite gave 5 Black normal-eyed young.

The most remarkable of the new developments was the *Clotted-eye* which arose in the F_2 of the *M. V* stock (**48**, p. 695–698, Fig. 1, *b* and *c*). The young were all hatched with perfectly normal eyes, but only a few remained normal. The irregularity showed itself soon after birth, but the rate of progression was very rapid. At first the eye looked as if the pigments had liquefied, and run together forming white patches above, and black patches below. Later on, the white pigment collected in clotted masses, with an occasional ommatidium showing—while in the final stages the white pigment increased so much in volume as to obscure the outline of the margin and the ommatidial cones completely. Sometimes the shape of the ommateum was broken and in consequence it became irregular and flattened out, sometimes it was unaffected under the bulging masses of white, as could be seen when the white pigment was dissolved out later. In extreme cases all the cells, retinular as well as interommatidial, appeared to have burst, the white pigment rising to the surface in clotted lumps, and the coloured sinking to the bottom, and collecting in little pools or patches of colour deep down.

Taking all the evidence into consideration, from this stock and from the reappearance of the form in the D. experiment and in later dredgings from the wild (p. 402), we came to the conclusion that the irregularity was in all probability caused by a thinness or weakness of the cell-walls, which sooner or later break down and liberate the cell-contents.

THE 1932 K. EXPERIMENT.

A dredging was brought in on Sept. 12, 1932, and several pairs were set out, but owing to adverse conditions the experiment was given up and is only mentioned here because two of the pairs gave some red-eyed offspring in the F_2 generation from their Outside matings.

One pair, *K. XXV*, 3 days after being brought in to the laboratory, extruded a brood of 12 Blacks. Intermatings in the brood bowl (7♂ and 3 ♀) gave 9 Black (2 spotted and 1 HN. spd.); 2 Dark Reds, and 3 Bright Reds. None survived.

Another pair, *K. XXXV*, extruded 7 days after capture a brood numbering 9 Blacks. One male and seven females reached maturity, and gave offspring as follows :—8 Black ; 8 Black and 1 Red ; 6 Black and 1 Red ; and 7 Black, 1 RB. and 3 Red.

In this stock, the eye-colour of the recessives was a full bright clear red, stable through life. Proof that it was indeed another appearance or the r_2 gene was obtained by crossing one of the F_3 females with a Red ♂ of *M. XVI* (r_2) when 18 young were hatched all with bright red eyes. These young also, intermating, produced similar red-eyed offspring.

THE 1933 D. EXPERIMENT.

The 1931 M. Experiment to test the wild stock for heterozygosity having failed through an outbreak of disease, another experiment on similar lines was started in February and March 1933 (**54**).

Half the animals were kept in an incubator at an air-temperature of 21° C., and half in an outside shed in or as near natural conditions as possible. As in the M. Experiment, the young hatched from eggs laid and fertilised in the wild, " Outside mating," were kept for comparison with the young from eggs laid and fertilised in the indoor conditions, " Inside mating."

Natural Conditions.

I. *Effects of extreme cold.*

The temperature of the shed in which the Gammarus were kept ranged from 25·8° C. to −1·5° C. For the first time the effect of continued low temperatures on the developing embryo was noted, as causing a delay or retardation of the rate of deposition of the black pigment. In many cases the action was completely inhibited till after extrusion, the young hatching out with bright red eyes, but in all the instances recorded the eyes darkened to black, usually before the first moult took place.

Another unexpected result of extreme cold during the embryonic growth was dwarfing, or retardation of body-development. The animals affected took months to reach maturity, and only a few gave offspring, partly owing to the difficulty of finding suitable mates, but partly also to the exhaustion of oviposition. The females were exceedingly small, and although the eggs were only one or two in number, yet they were normal-sized ; the young also which hatched from them were the usual size and developed normally.

II. *Changes in the interommatidial and retinal pigments.*

The variations in the white pigment included in addition to the numerous sporadic cases of partial or complete Nowhites, the two definite

Nowhite types, Genotypic and Phenotypic. Gradual Nowhites, with the steady reduction of white pigment from normal to Nowhite, also occurred, as well as Gradual Normals, with the steady increase of white from Nowhite to normal. But perhaps the most interesting observation was the effect of the low temperature on the embryonic eyes. The laying-down of the white occurs normally in the later stages of development, but during the extreme cold the rate of its deposition was slowed down to such an extent that the young were born with no trace of white in their eyes, the same effect as with the melanic pigment. In the same manner the rate accelerates after extrusion so that the deficiency is made good, in a longer or shorter time, according to the temperature.

Changes in the *retinal pigment.* The r_2 gene reappeared in four stocks, *D. XXXI*, *XLVI*, *LIII*, and *LXIV*.

In *XXXI* and *LXIV* it was carried by the female and segregated out in the F_2 of both Outside and Inside matings ; in *XLVI*, also in the F_2, probably carried by the male.

In *LIII A.*, for the first time in the work, Red-eyed recessives appeared *in the F_1 from the wild*, proving both parents to have been heterozygous for Red. The female was mated with 3 other males, homozygous for Black, and the recessives appeared in the F_2 from all these matings.

Three other stocks gave Reds, *D. VIII*, *XVIII*, and *XXIX* ; the first was shown to be distinct from Stocks I and II ; the others died out untested.

A new variant type, *D. X*, arose, which bears a great resemblance to the Lilac Stock *XX* (p. 393) ; in the eye-colour of the recessives, the two types, Creamy and Reddish Lilacs, being represented ; in the pale pigmentation of the gonads and eggs ; and in the variations of the white pigment from excess to complete absence. This stock is still breeding, but the recessives are so few and so delicate that no knowledge of its genetic position has yet been obtained.

INCUBATOR CONDITIONS.

I. *Effect of high temperature.*

The incubator was kept at approximately 21° C., but while the Gammarus will live and breed at this temperature for a time it is evidently too high, the stocks tending to die out within a generation or two.

The time of incubation from oviposition to extrusion from the pouch was practically constant for the F_2 as well as for the F_1, 9 days being the usual period. The time taken in development, however, was surprisingly long, as long in fact as in the " Natural Conditions " part of the experiment. The F_2 broods were small and feeble, with few survivors, but when, later, the remnants of the heterozygous stocks were removed to laboratory temperature, they recovered strength and became established.

II. *Changes in the interommatidial and retinal pigments.*

Changes in the interommatidial pigment were very frequent, with the tendency always towards reduction of the white pigment. Nowhites, Half Nowhites and Spotted occurred in many stocks, and Clotted-eyes were found.

The changes in the retinal pigment numbered 4, all reappearances of the r_2 gene in *dd. XXXIX*, *XLIII*, *LXX* and *LXXIII*.

One of these stocks, *dd. LXXIII*, is noteworthy as being the second instance of a recessive appearing *in the F_1 from the wild.* Out of 43 F_1 young hatched, one had the right eye bright red and the left eye black. It functioned as a heterozygous Black, giving 102 Black to 34 Red when mated with heterozygous Black females, and 23 Black to 41 Red in three matings with F_2 Red females.

FIRST APPEARANCE OF CLOTTED-EYES IN THE WILD

The Clotted-eyes arose in Stock V of the M. Experiment (p. 399). The character proved heritable, and still is, in the Laboratory cultures. There seems, however, to be another form of this variation, indistinguishable from the type in appearance, but genetically different. Similar instances have been recorded from time to time ; for example, the heritable White-eye of Stock II compared with the non-heritable White-eye of Stock I (**4**, p. 287) ; the two forms of Nowhite, Genotypic and Phenotypic ; and now this case of the heritable and non-heritable Clotted-eye.

The dredging in which the latter type was first found in numbers was brought in from the wild on January 15, 1935. Out of a total of 301, 220 were normal-eyed and 81 clotted. A second dredging taken on February 12 gave 189 normal to 35 clotted.

The F_1 and F_2 generations from matings of normal-eye×clotted, and clotted×clotted, consisted of normal-eyed young only. Experiments are still being carried on, but so far no sign of the clotted variation has shown itself in any of the offspring.

FIRST APPEARANCE OF RED-EYE RECESSIVE IN THE WILD

Though heterozygosity had now been definitely proved to exist in the wild population, yet all the known homozygous recessive animals came from cultures in the laboratory : none had yet been taken in the wild.

In 1935, however, the final proof was obtained, and a Red-eyed recessive was brought in from the ditches (**47**, p. 836).

It became a male, and was found to carry the r_2 gene (stable colour). Mated with a Red female from Main Stock II it gave a brood of 9 Red. It was next tried with a Red Nowhite female of Stock I, the result being 20 Black young. Mated again with a female from *MM. LXIX* Stock (r_2 stable colour) it gave 14 R.

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* Printer's error on page 202, line 24. The line should read: "white II ♀ mated with red ♂ gave white young."

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APPENDIX I.

Professor Huxley in *Problems of Relative Growth*, 1932, p. 40, referring to the work on the Moulting and Growth-stages of Gammarus, 1924, says: "Sexton states that sexual maturity occurs at the seventh instar, that proportions continue to change for two further instars in the male, one in the female, but after this no further proportion-changes occur (though the males at least may increase about 40 per cent in length). That this statement is not accurate is shown by Kunkel and Robertson, whose graphs demonstrate a change in the proportions of several organs up to the largest sizes found."

A reference to the paper mentioned (**12**, pp. 352 and 387) will show that what I actually stated was that sexual maturity was reached at the eighth growth-stage; that the differentiation of the characters (not "proportion-changes") stopped there in the female, but continued in the male for two more growth-stages before the "definitive adult male" form was reached; that sexual maturity was attained at about half-growth and that thereafter the characters now assumed by both sexes were preserved unchanged through the rest of their lives, except for the increase in size till the maximum growth of the species was reached. And finally that there is a fixed definitive form, and a definite maximum size.

Professor Kunkel (**22**, p. 657) says of his work that "it is fully realised that the method of studying growth of an organism by measuring a population, as has been done in the present study, is open to certain objections from which the study of successive ecdyses of the same individual is free." I agree with him, especially when the method is applied to an animal like *G. chevreuxi* in which growth is accomplished in a series of definite stages, with each stage essentially constant in its characters, and differing in the relative proportions of the parts from the other stages.

The great objection, of course, as he points out, to studying the question by means of the successive ecdyses of one animal is the difficulty of obtaining complete series through the " tendency of the animal to eat its own skin very shortly after shedding it," added to which is the impossibility of mounting the fragile sloughed-off moults without distortion. On the other hand, the results of the second method, measuring a population collected at random cannot be considered free of error. Besides the different line of development of the male and female at sexual maturity, and the variation in the proportions of the different parts during that period, there are other difficulties likely to confuse the issue. Take, e.g., the secondary sexual characters the antennæ, the first and second gnathopods, the first peræopod, and the third uropod, which are used in specific distinction. Certain of these, such as the antennal flagella, and the rami of the third uropods in particular are very liable to injury, and are frequently broken, and are then replaced by regeneration, but though the regenerated part is eventually restored to normal size the process is a gradual one and requires time to bring it into line with the rest of the organism.

An instance of how misleading this can prove in an argument may be quoted from Professor Kunkel's paper (p. 658).

He says that " in general sexual differences could not be determined at as early a stage as Mrs. Sexton has shown in the careful drawings of successive moults of the same individual. The characteristic curved hairs of the second antenna of the male do not appear generally as early as she has figured them," and then he cites the measurements of the smallest individuals whose sex he could be sure of, " the flagellum of the first antenna in one case had only ten segments which would correspond with Mrs. Sexton's fourth stage "—whereas the true explanation is, that if a sexually mature individual had only ten joints in the flagellum it would mean, *not* that it was at the fourth growth-stage, but that at some previous stage the flagellum had been broken and was regenerating, but had not yet caught up to the other parts—that it had in fact only arrived at the fourth stage, with several stages still to go before reaching normality.

My paper was mainly concerned with figuring and describing the development of male and female from birth to the attainment of sexual maturity at half growth, and though measurements were taken of the older stages, they were not included. If, however, the aim had been to study the relative growth of certain parts through life an equally accurate but much easier method could have been employed. By preserving one or two specimens at each stage a complete developmental series could have been formed, from birth to sexual maturity, from maturity to maximum growth and then to maximum length of life. The measurements of such a developmental series of male and female apply to all males and females of the species. The striking point which emerged from the work on the moults was the *constancy* of each stage of development; size might vary according to the temperature during growth, but the relative proportions of the body and appendages at each stage remained unchanged.

The two series of drawings referred to (ten of the male, and eight of the female), while taken as far as possible from two individuals, are in fact representative of a very large number of animals. Each moult, as it was cast, was compared detail by detail with the same stage in all the series kept under daily observation. Three thousand moults were examined in this way, and drawings made, of which over three hundred are still in the laboratory, in addition to those figured in the paper.

E. W. S.

APPENDIX II.

DETAILS OF THE DIFFERENT MATINGS IN THE LILAC STOCK *XX*, 1931 M. EXPT., (see p. 396).

The **Lilacs** were all derived from two heterozygous animals, the male and female of *Pair 6*. The male was mated also with two homozygous females, with one of which he gave 120 Black (2 Half-Nowhite), no survivors, and with the other, 14 Black, from which the Lilac reappeared in the F_3 (p. 394).

Details of the Pair 6 mating. The offspring of this pair consisted of Black and Lilac in a 3 : 1 ratio, viz. 190 Black to 66 Lilac. The first brood was 3 Black. The next three consisted of Blacks and Lilacs, 7 B. to 4 L., 8 B. to 2 L., and 4* B. to 3 L. The 9 Lilacs were characterised by pale clear lilac colour and heavy white reticulation. None of them survived to maturity, but it was noted that the amount of white pigment lessened with growth.

Male 6 having been put with 2 females to test them for heterozygosity, female 6 was mated with another male, and had 20 Black-eyed young, all of which died immature.

After an interval of six weeks, the pair were put together again, and had 10 more broods, 168 Blacks and 57 Lilacs (viz. *6 B. to 1 L., *12 B. to 7 L., *13 B. to 7 L., 12 B. to 5 L., *16 B. to 5 L., 16 B. to 3 L., 17 B. to 4 L., 30 B. to 7 L., 20 B. to 9 L. and 26 B. to 9 L.).

* Broods examined directly after extrusion; the others within two or three days.

The different F_2 *matings* and their offspring are as follows:

Group 1. Black × Black which gave all Black offspring. There were 12 matings in this group, 6 mixed matings in the brood-bowls and 6 of separate pairs. The numbers in the broods were small, viz. 11, 1, 9, 16, 2, 2, 2, 14, 4, 8, 19, 1 and 4, 7, 8, 6, 12, 5. The last 6 broods came from one pair, the eggs were normal dark green in 3 broods, but in the 3 following the colour was a pale eau-de-nil shade.

Group 2. Black × Black matings which gave Black and Lilac offspring. Mixed matings from three brood-bowls, 28 Black to 6 Lilac. From *174 a bowl*, *3 Black and 1 Lilac (*314*†); two of the Black survived and mated. The female laid one batch of the *white-eggs* mentioned above, but none hatched. Reduction of the white pigment took place in both, in the female as far as the complete nowhite condition. The Lilac became a ♀ and was mated but with no results.

From *236 a bowl*, 11 Black and 1 Lilac (*289*). The Blacks in mixed matings gave 11 Black (*352*), which in the next generation produced 28 Black (13 spotted), none of which survived.

The Lilac →♂ was tried with 1 Lilac, and 1 Black female, with no results; with a second B. ♀ it had 26 Black (3 spd.), none survived.

From *299 a bowl*, 14 Black and 4 Lilac (*426*). None survived.

Group 3. Black × Black matings which gave Black, Lilac and Nowhites.

From *174 a bowl*, 9 Black normal, 1 Black Nowhite, 1 Black Half-Nowhite, 4 Lilac and 1 Lilac Nowhite spotted (*395*). This is the first record of the Dark Lilac Nowhites, only 5 of which were found in the stock, this one and the 4 mentioned below (*see 414*). It was left in the bowl with the Lilacs; later, 1 young Lilac was found (*517*).

Group 4. Black × Lilac matings which gave Black and Lilac. Two matings.

From one pair (*194 a and b*) Black ♂ × Lilac ♀, 7 Black and 3 Lilac (*396*).

From another (*194 b. 2*) Lilac ♂ × Black ♀, 2 Black and 2 Lilac (*430*). None survived.

Group 5. Lilac × Lilac matings which gave Lilac and Lilac Nowhite. There were 6 mixed matings in the different brood-bowls, 5 giving 103 Lilac, and 1 giving 19 Lilac and 4 Lilac Nowhite, and 2 matings of separate pairs, giving 28 Lilac young.

In these matings, the distinction between Creamy and Reddish Lilacs was first noted.

The details of the F_3 *broods* are as follows, with the colour of the survivors and their offspring if any. Numerous matings were made with no results.

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* See footnote on p. 409.

† The brood numbers italicised and in brackets refer to the records of the stock kept in the Laboratory.

From *194 b. bowl.* 35 Lilac (8 spotted) (*328*). Only 2 survived to maturity, both females, one the typical Creamy Lilac, the other, Reddish Lilac. No results.

From *221 b. bowl* there were several broods and one from a separate pair. The first brood consisted of 6 Lilac (*281*); three survivors, 2 males and 1 female, all the Creamy Lilac colour. No results. The second brood of 18 Lilac (*325*); the 5 survivors were 1 female Creamy Lilac, 2 males and 2 females Reddish Lilac. The mixed matings in the brood-bowl gave an interesting result: 25 young were found of various sizes, consisting of 11 Creamy (3 spd.) and 14 Reddish (7 spd.). The third brood, 14 Lilac (*338*), had no survivors. The fourth brood, 2 males, spotted, mature when found (*530*), one, Creamy Lilac, with a little of the white reticulation still remaining, and one very Reddish Lilac. No results.

From *221, Pair 1.* Eleven Lilac (4 spd.) (*326*); 4 survivors, all the Creamy Lilac shade. Later, in one of these, a male, the Creamy tint became slightly flushed with pink.

From *236 b. bowl* 14 Lilac (3 spd.) (*312*); ten survivors, Creamy Lilac (one later developed the pink flush). Two females were mated with the Lilac Nowhite ♂ *414 b.* (see below), and had 2 broods, 3 Lilac (1 spd.) (*522*); and 8 Lilac (4 spd.) (*523*.) One brood, mixed mating, 2 Lilac spd. (*378*).

From *253 Pair 3.* 17 Lilac (*348*) Dead.

From *266 b. bowl.* 7 Lilac (*340*) Dead.

From *317 b. bowl.* 7 Lilac (*440*) Dead.

Group 6. Lilac × Lilac mating which gave Lilac and Dark Lilac Nowhite.

From *236 b*♂×*282 b* (3♀♀) 19 Lilac and 4 Lilac Nowhite (*414*). Survivors were—Lilacs, 3 males (2 spd.); 2 females spotted; and 7 nearly mature (4 spd.) all still lilac; two others, males, had changed colour, one spotted was now a Dark Lilac Nowhite, and the other Dark Lilac Half-Nowhite. One brood was hatched from mixed matings, of 14 Lilac (4 spd.) (*481*) from which a mating was made with Stock *XX* (Inside mating), p. 413.

Two of the four Lilac Nowhites survived, but one was eaten by its mate; the other was mated with two Lilac females and gave offspring. (See above, under *236 b*).

F_4 Matings.

From *Group 3* Black×Black giving Black, Lilac and Nowhite. One brood (*517*) of 1 Lilac→♀ Reddish Lilac with flecks of white reticulation. Eaten by mate.

From *Group 5* Lilac×Lilac giving Lilac. Two broods (*507*) and (*559*) 11 Creamy Lilac (3 spd.) and 14 Reddish Lilac (7 spd.) of various sizes from mixed matings of Creamy×Reddish. They were divided into 5 bowls according to size and colour, as follows :—(*a*) 5 larger Creamy Lilac→three males and two females. All developed a slight "pink flush" later. Mixed matings gave one brood (*545*) of 3 Lilac with colour rather redder than usual. (One survived for a short time→Creamy Lilac with a pink flush and some white reticulation.) In (*b*) bowl, 5 smaller Creamy Lilac, with the pink flush. Two survived, ♂ and ♀, both with reddish flush and some white reticulation. No results. In (*c*) bowl, 9 larger Reddish Lilac→6 males and 3 females. Mixed matings gave 4 Reddish Lilac (*564*) very small (three showing white reticulation, and the fourth with hardly any white, but with the dark rings around the ommatidia). Later, the one survivor, a spotted ♂, still Reddish Lilac, was tried with three females. No results : females eaten. In (*d*) bowl, 5 smaller Reddish Lilac. One survivor, a female, still Reddish Lilac with more white than usual. No results. One brood in (*e*) bowl (*559*), 1 Creamy Lilac→♂. No results.

From the same *Group 5* 1 brood (*378*) of 2 Lilac spotted was hatched. One survivor ♀, Creamy Lilac shade. No results.

And 2 broods, from Lilac females×Lilac Nowhite ♂ (*414*), viz. (*522*) of 3 Lilac (1 spd.)→Reddish Lilac in four to five weeks ; and (*523*) 8 Lilac (4 spd.). All died.

From *Group 6* Lilac×Lilac giving Lilac and Lilac Nowhite. One brood from mixed matings of the Lilacs, 14 Lilacs (4 spd.) (*481*). From this brood a Creamy Lilac ♂ was taken for a mating with Stock XX (i.e. the stock from ♀ XX's Inside mating) which had given nothing but Blacks (see p. 413).

Details of the Pair 2 Mating. This was a mating of the heterozygous ♂ 6 with the homozygous ♀ 2 which gave an F_2 of 14 Black.

The F_3 consisted of 76 Black and 4 Lilac—viz, 6 broods of Black,11 : 4 : 12 : 4 : 8 : 6 and 4 broods from one pair, of 31 Black and 4 Lilac.

Only 2 of the Lilac survived, ♂ and ♀ Creamy Lilac. No results ; the male ate this female, and two Black ones with which it was being tested.

In the F_4 generation mixed matings gave 53 Black and 10 Lilac, including 2 Dark Lilac ; and matings of 3 pairs gave 60 Black and 13 Lilac.

The Lilac-eyes in the descendants of *Pair 2* were of exactly the same types as in those of *Pair 6*.

Crosses made with Stock I Red Nowhite, Stock II Red and Stock *LVII* Nowhite-Red :—

With Stock I. A Creamy Lilac F_4 ♂ with pink flush was mated with a Red Nowhite ♀ of Stock I, and gave one brood of 7 Black (3 spd.). These, mated *inter se*, gave 10 young in the next generation, viz. 3 Black and 1 Black Nowhite, 2 Reddish Black, 3 Red and 1 Lilac of the Reddish Lilac type with more white reticulation than usual.

The ten were mated together as much as possible, and produced an F_3 as follows :—

Black ♂ by Black ♀ had 7 Black (3 spd.) and 7 BN. offspring ; the same Black ♂ mated with the BN. ♀ gave 12 Black and 12 BN. ; one Red ♂ mated with this same BN. ♀ and produced 36 young (of various sizes when examined), 3 Black, 11 BN., 5 Dark Reddish Lilac Nowhites, 3 Dark Red and 14 RN.

The 2 Reddish Blacks became Black with only a slight reddish tinge and gave Black and Red in the proportion of 3 : 1.

The 1 Reddish Lilac became a ♀ and mated with one of the Red males and had a brood (*604*) of which only 2 survived, 1 B. spd.→♂ and 1 Red spd. (not a clear red, but more of the Inter. Red shade)→♀.

The (*604*) ♂ and ♀ mated and 4 broods were produced, viz. 2 Black (1 spd.) ; 2 Black (1 spd.) and 2 RN. ; 3 Black (1 spd.), 1 Dark Reddish Lilac and 2 Red spotted ; 1 Black, 3 BN. and 3 Red (survivor→Int. Red).

It is noteworthy that the Creamy Lilacs have not yet appeared in this cross stock.

With Stock II Red. A Creamy Lilac F_4 ♂ was mated with a Red ♀ F_3 *MM. LXIX* Stock (r_2 gene) and had 46 Black offspring (4 spd.). None survived.

With Stock LVII Nowhite-Red. A Creamy Lilac F_4 ♂ was mated with two Nowhite-Red F_4 Stock *LVII*. They mated several times but only one brood was produced by each female, viz. 1 Black spotted, died ; and 4 Black, all spotted.

The 3 Black survivors were a male, and 2 females which mated, one ♀ giving 5 Black, 1 Dark Red and 3 nowhite Red young ; the other, 3 Black (1 spd.), 1 Dark Red and 1 nowhite Red, all of which died before maturity was reached.

Cross between the XX Stocks. " Outside " and " Inside." A cross was made with a Creamy Lilac ♂, F_4 of the Outside Stock, mated with an F_3 Black ♀ from the Inside Stock (of the same parent female *XX*), which had given only Black-eyed normals and an occasional Black Nowhite.

One brood was hatched, consisting of 13 Black (2 spd.). These interbred, but from their matings only 7 young were produced, 6 Black (2 spd.) and 1 BN., a number too small to be conclusive.

The next generation, F_3, consisted of 16 Black and 4 Reddish Black, two of these almost dark red in colour.

The F_3 Blacks were mated together, giving only the normal black-eyed in the F_4, but in the F_5 the Lilac appeared, one brood consisting of 4 Black and 3 of the " Reddish-Lilac " type with partial white reticulation. These died without offspring.

The F_3 Reddish Blacks became darker, i.e. black with a slight tinge of red. All survived, two males and two females, and gave a large F_4

containing a great variety of colour, Black, Reddish Black, Dark Red, Dark Red Nowhite, Dull Red, Lilac Nowhite, Reddish Lilac, Intermediate Red, and deep Red, but no Creamy Lilac appeared in this, or in the following generations as far as the work has gone.

The changes in colour in the F_4 and F_5 generations covered an equally wide range :—**B**. remained unchanged ; B→slightly reddish ; B→DR ; B. lightened to Int. Red ;

RB unchanged ; RB→B ; RB→R. Purple→Purple Black ;

DR unchanged ; DR→P.B→B ; DR→R.P.→P.B. ; DR→Dark Lilac : DR→Reddish Lilac with white reticulation :

DR Nowhite→Dark Lilac Nowhite :

Dull Red→Reddish Lilac :

Reddish Lilac →some with broken white reticulation, some with perfect reticulation, and others, a new combination, with the white reticulation but with the dark rings also, round the ommatidial cones, characteristic of the Creamy type in the Main Stock :

Int. Red→Reddish Lilac ; and the **Deep Red**→Reddish Lilac.

Abstracts of Memoirs.

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

The Determination of Zinc in Water by means of Sodium Diethyldithiocarbamate.

By W. R. G. Atkins.

Analyst, Vol. 60, 1935, *pp.* 400–401.

Zinc may be estimated turbidimetrically in water supplies, in concentrations of from 0·02 to 25 parts per million, using a 0·1 per cent aqueous solution of the reagent. The turbidity disappears in ammoniacal solution, but a turbidity caused by lead does not. Iron may be removed as described by Callan and Henderson. A sample of water from a galvanised iron tank was found to contain 5 p.p.m. For the estimation of zinc in sea water see this Journal, Vol. XX (No. 3), p. 625.

W. R. G. A.

Photo-electric Measurement of Submarine Illumination : an Outline of the Methods and their Results.

By W. R. G. Atkins and H. H. Poole.

Report of Fifth Pacific Science Congress, III, 1933, *pp.* 2129–2139.

Since reviews of the subject in general had already been given in the Journal of the International Council for the Exploration of the Sea (Atkins, 1926 and 1932), the present review deals mainly with recent work. Two methods are suitable for use at sea in a small ship under average weather conditions. Seasonal changes have been studied and the penetration of light of various wave-lengths from dark red to ultra-violet has been measured. The results have applications in the study of photosynthesis, the movements of the zooplankton, and the production of vitamin D.

W. R. G. A.

The Photo-electric Measurement of the Diurnal and Seasonal Variations in Daylight and a Globe Integrating Photometer.

By W. R. G. Atkins and H. H. Poole.

Phil. Trans. Roy. Soc., London, A, **235**, 1936, *pp.* 245–272.

The exposure of plane, tubular and spherical surfaces are considered in relation to the measurement of daylight by sodium, potassium and selenium cells, and by photo-sensitive liquids. Curves show the variation of the sensitivity of the cells with wave-length in a mean noon sunlight spectrum. A Burt sodium cell and a Cambridge "thread recorder" were used to get daily records, twenty of which are reproduced. The curves for 1930 have been measured to give vertical illumination integrals in kilolux hours. The monthly percentages of the annual illumination integral ranged from 1·25 for December to 16·0 for July. The ratio of vertical sunlight to vertical sky light ranges up to about 3·0, as found with a sodium cell. Much larger ratios are obtained with a selenium cell. The vertical illumination with sun at 45° varies greatly, even on cloudless days, but averaged 102 kilolux, using a sodium cell. A globe photometer is described, which by means of a horizontally mounted selenium cell and triple diffusing surfaces gives readings independent of the altitude and azimuth of the source.

W. R. G. A.

The Developmental Stages of Three English Barnacles.

By R. Bassindale.

Proc. Zool. Soc., London, 1936 (1), *pp.* 57–74.

In an attempt to determine the life-history of the common English barnacles, cultures of each of six species were set up. The three successful cultures showed a marked plant growth. The three species reared (*Balanus balanoides* (Linn.), *Chthamalus stellatus* (Poli) and *Verruca strœmia* (O. F. Müller)) each had six naupliar or metanaupliar stages. This is followed by a cypris stage which settles on the sub-stratum and metamorphoses into the young adult. This development accords with the previous accounts of the life-history of *Balanus perforatus* Brugière and *Lepas fascicularis* Ell. & Sol., but not with that of *Balanus crenatus* Brugière in which Herz found eight stages prior to the cypris.

Development, excluding the duration of the cypris stage, takes from two to three weeks. The successive stages show gradually increasing size and complexity of setation.

The sizes and setation of each stage are given together with notes on the discrimination of the larvæ of different species and on the breeding periods of the adults.

R. B.

The Action Potentials in Maia Nerve before and after Poisoning with Veratrine and Yohimbine Hydrochlorides.

By L. E. Bayliss, S. L. Cowan and Donald Scott, Jr.

J. Physiol., Vol. LXXXIII, 1934, *pp.* 439–455.

The action potentials were recorded by means of a paraphase fed push-pull output amplifier, driven from the A.C. mains, and a moving iron oscillograph. In nerves from the walking legs of *Maia squinado* there are at least two sets of fibres in which impulses are conducted with very different velocities. At 12° C. the velocity of the faster impulse is about 2·5 m. per sec. and that of the slower impulse about 1·0 m. per sec. Nerves poisoned with veratrine show a prolonged after-potential which begins immediately after the spike, rises slowly for at least 200 msec., and gradually disappears in half an hour. Nerves poisoned with yohimbine show a positive after-potential, immediately succeeding the spike potential, which may last up to 0·2 sec.; these are not due to changes in the depolarized region, since they can be produced by treatment of the uninjured part of the nerve.

L. E. B.

Some New Forms of Visual Purple found in Sea Fishes, with a Note on the Visual Cells of Origin.

By L. E. Bayliss, R. J. Lythgoe and K. Tansley.

Proc. Roy. Soc., London, B, CXX, 1936, *pp*. 95–113.

A number of new forms of visual purple have been found in sea fishes, which have maxima of absorption between 505 mμ and 545 mμ. The absorption curves were obtained by a null-point photoelectric spectrophotometer, which is capable of giving accurate readings with 0·5 c.c. of solution and with a light intensity insufficient to bleach the visual purple. Alterations in the form of the absorption curve may occur as a result of "bleaching" of yellow substances in the control (bleached visual purple) solutions; alterations may also occur as a result of extracting with distilled water instead of digitonin.

A histological examination of the retinæ was made. The relative numbers and structure of the rods and cones; the movements of the visual cells as a result of light- and dark-adaptation; the movements of the pigment epithelium; and the staining reactions for visual purple are described.

The variety of visual purple carried by a species can be related neither to the available data on the depth which that species normally frequents, nor to the ancestry of the species, nor to the histology of the retina of origin.

L. E. B.

Action Potentials in Nerve of Sepia.

By J. Yule Bogue and H. Rosenberg.

J. Physiol., Vol. LXXXIII, 1934, *pp.* 21P–22P.

The action potentials of the fin and stellar nerves (postganglionic fibres of the stellate ganglion) were recorded. The central ends of these nerves were stimulated electrically (i.e., the preganglionic fibres in the ganglion preparation). Both nerves showed a fast and a slow wave, but the time relations were different in the two cases. In the stellar nerve the fast wave rises to its peak in 0·8 msec. and lasts 2 msec. The following slow wave attains its crest in 2·5 msec. and continues for 8 msec. The maximum negativity is 3 and 2 mV. resp. With a strong stimulus a second quick wave is obtained which is generally superimposed on the slow wave. Apparently the fast and the slow wave are independent. They originate in the stellate ganglion since stimulation of the stellar nerve gave no appreciable antidromic impulse. Owing to the synaptic delay the velocities of the waves from mantle connective to stellar nerve appear to be small: 3·5 m. per sec. for the fast and 2·3 m. per sec. for the slow wave. In the fin nerve the time relations of the fast wave are of the order of those of the slow wave in the stellar nerve. But its velocity is comparatively high (5·1 m. per sec.) and decrementless in fresh nerves; that of the slow wave is 2·6 m. per sec. During repetitive stimulation the absolute refractory period of the quick fibres is shorter than 5 and longer than 2·5 msec. It is suggested that the fast wave of the stellar nerve is generated in the giant fibres and associated with rapid movements of the mantle muscle.

H. R.

Electric Excitation of the Fin Nerve of Sepia.

By L. Bugnard and A. V. Hill.

J. Physiol., Vol. LXXXIII, 1935, *pp.* 425–438.

The action currents of the mantle connective nerve of Sepia, entirely non-medullated, have been measured with a moving coil galvanometer in response to low frequency repetitive stimulation.

The strength-duration curve is of usual form, the quantity of electricity required for constant excitation becoming constant at short times. At 20° C. "the characteristic time" for excitation by minimum energy is 3 to 5 msec., about ten times that for frog's sciatic.

Distance between electrodes has little effect on the strength-duration curve within the range 1·5–20 mm. Size of stimulating electrodes, frequency of excitation have little or no effect. Transverse excitation with linear fluid electrodes, has a large effect, reducing " the characteristic time " to one quarter of that for longitudinal excitation.

The injury potential of the fin nerve is about 20 mvolts. It can be reversibly reduced by increased K-ion concentration. Increased K reduces or abolishes excitability but does not change the form of the strength duration curve. The nerve can be fatigued, recovery occurs in air.

L. B.

A System of Rational Units for Reporting Nutrient Salts in Sea Water.

By L. H. N. Cooper.

J. Cons. int. Expl. Mer., Vol. VIII, 1933, *pp.* 331–334.

The milligram-atom of minor constituents per cubic metre of sea water is proposed as unit of measurement, e.g., the milligram-atom of P would be used instead of the mg. of P, P_2O_5 or PO_4'''. It is claimed that the proposed system would much simplify the reporting of data and that it employs the unit used by plants and animals in building up their structure. Tables are given to show the effect of the change.

(Following the publication of this paper, the subject has been considered *in extenso* by a sub-committee of the International Council.)

L. H. N. C.

Iron in the Sea and in Marine Plankton.

By L. H. N. Cooper.

Proc. Roy. Soc., London, B, CXVIII, 1935, *pp.* 419–438.

2:2′:2″-Tripyridyl, recently prepared by Morgan and Burstall, forms a co-ordination compound with ferrous-iron possessing an intense violet colour. This has been applied to the direct determination of iron in sea water. Without preliminary concentration 1 mg. per cubic metre (1γ per litre) of Fe may just be determined and conditions may be adapted for the determination of ferrous-iron, " reducible iron," which includes ferrous- and ferric-ions and some of the iron in suspension, total iron present in all forms, total iron in water freed from particulate and much of the colloidal iron by passage through a Zsigmondy membrane filter and, by difference, iron in particulate form. The method is sensitive, reliable and rapid and fluorides do not interfere.

The amount of iron in true solution as ferric and ferrous ions is very small, probably less, possibly much less, than 2 mg. per cubic metre. Most of the iron is present in particulate form, the amount of which varies greatly. The probable formation of ferrifluoride and its effect on the iron system is discussed. Thermodynamic data for the hydroxides have been used to derive the limiting solubilities of ferrous- and ferric-ions in sea water. The concentration of free ferric-ion has been found unlikely to exceed 10^{-12} mg. per cubic metre.

Seasonal determinations have been made with 2:2′-dipyridyl on the amount of iron in quantitative catches of plankton and compared with the amount of phosphorus. Diatoms require several times as much iron as phosphorus whereas the iron requirements of zooplankton, particularly Ctenophores, are much smaller. The plankton catches were richest in iron at the height of the spring diatom outburst. When the plants are eaten by herbivores, the excess of iron over requirements is excreted and becomes available more or less quickly for another growth cycle. A diagram is given illustrating tentatively the cycle of iron in the sea.

L. H. N. C.

The pH and CO_2-combining Capacity of Maia Blood.

By S. L. Cowan.

J. Physiol., Vol. LXXXIV, 1935, *pp.* 53P.–54P.

Kerridge determined the pH of Maia blood at various partial pressures of CO_2 and found that CO_2-binding capacities calculated from her figures were in agreement with the experimental volumes determined by Parsons and Parsons if it was assumed that pK, in the Henderson-Hasselbalch equation had a value of 6·5 at 13° C. However, Buch, Harvey, Wattenberg and Gripenberg have shown that the use of the Henderson-Hasselbalch equation to calculate pH values of sea water is justified only if a correction is made for the depressant effect of the salts present on the activity of the bicarbonate ion. If a similar salt correction be applied to Maia blood, which is approximately isotonic with sea water, then the pH figures calculated from Parsons and Parsons results are 0·4 pH unit lower than those determined by Kerridge. If the discrepancy is real, it is in the wrong sense to be explained by the formation of unionized carbon dioxide-hæmocyanin compounds.

S. L. C.

Quaternary Ammonium Salts and the Action Currents in Nerve.

By S. L. Cowan and H. R. Ing.

J. Physiol., Vol. LXXXIV, 1935, *pp.* 90–110.

The following solutions of purified quaternary ammonium salts were without effect on the action current in Maia nerve : tetramethylammonium iodide, 1-50 millimols per litre ; tetramethylammonium chloride, 1-50 millimols per litre ; strychnine methiodide, 1 millimol per litre ; strychnine ethiodide, 10 millimols per litre. Curarine chloride, 5 millimols per litre was also ineffective. Silver chloride saturated sea water depressed the action current in crab nerve slightly. A 50 millimolar solution of tetramethylammonium chloride in silver chloride saturated sea water or a 5 millimolar solution of curarine chloride in silver chloride saturated sea water abolished the action current.

A solution containing 10 millimols per litre of purified tetramethylammonium chloride or 3 millimols per litre of curarine chloride did not curarize crab nerve-muscle preparations.

The following solutions of purified quaternary salts were without effect on the action current in frog nerve, even when the nerve was asphyxiated after the poisoning and allowed to recover in oxygen : tetramethylammonium chloride, 2 millimols per litre ; tetramethylammonium iodide 2 millimols per litre ; octyltrimethylammonium iodide, 2 millimols per litre ; strychnine methiodide, 1 millimol per litre. However, contact of any of these solutions with solid silver chloride could render them effective in diminishing or abolishing the action current : this explains Cowan and Ing's previous results (1933), and carefully purified salts are without effect.

Tetraethylammonium iodide solutions probably increased the area (galvanometer deflection × time) in crab nerve and certainly did so in frog nerve. In the latter case asphyxiation did not augment the effect.

S. L. C.

The Life History of Sacculina.

By J. H. Day.

Quart. Journ. Micr. Sci., Vol. 77, 1935, *pp.* 549–583.

From the statistical analysis of a year's samples of an infected population of the crab *Portunus holsatus* Fabricius it was concluded : first, that crabs may be infected by Sacculina at any age ; secondly, that the developmental sequences in the life history of the parasite are dependent not on the season but possibly on the phases of the host ; thirdly, that the internal development of the parasite lasts nine months, and that the first batches of larvæ appear three months later.

Two separate experiments showed that the evagination of the parasite does not take place at an ecdysis of its host.

It is suggested that an anomalous group of highly modified male crabs without externæ but containing living parasitic roots are " scarred crabs " that have moulted ; further, that such modified crabs will in time regenerate externæ. Experimental and histological evidence supports this suggestion, but it is not held that the theory of regeneration is completely proved.

An account is given of the effects of Sacculina on the secondary sexual characters of *Portunus holsatus.* Only male crabs are dealt with. It is shown: (*a*) that various degrees of modification are possible; (*b*) that the percentage of infection increases among large crabs; (*c*) that the smaller the crab the greater the liability to maximum modification; (*d*) that the maximum amount of modification which is possible decreases among larger crabs.

J. H. D.

The Irritability of Non-Medullated Nerve.

By R. W. Gerard.

J. Physiol., Vol. LXXXIII, 1934, *pp.* 24P.–25P.

The irritability of the non-medullated leg nerve of Maia was explored with rectangular or condenser current pulses of various intensity, duration and frequency, the action potential of the nerve serving as indicator of response.

The time characteristics are very long—even at 0·5 sec. duration no true rheobase is reached; and whereas the response to alternately directed short intense stimuli at 220/s is double that to unidirectional ones at 110, the response is entirely wiped out if longer weaker pulses are used. At shorter times, the voltage-duration curve tends to become straight (log-log plot) with a slope near, but less than, 45°. In this, as also in the influence of interelectrode distance and of cathode size on the curve, this non-medullated nerve resembles myelin-free muscle rather more than it does medullated nerve.

R. W. G.

Chloride and Total Osmotic Pressure in the Blood of Marine Teleosts.

By Allan L. Grafflin.

Biol. Bulletin, Vol. LXIX, 1935, *pp.* 245–258.

An effort has been made in this study to obtain data upon the plasma chloride and total osmotic pressure (delta) of the blood of marine teleosts under their normal conditions of existence in the sea. For this purpose hook-and-line specimens, bled immediately after catching, have been used as the best available material. Studies upon pollack, cod, sculpin, flounder, mackerel, and conger indicate an appreciable physiological range of variation in both chloride and delta, with no detectable correlation between the two in any given species. The average plasma chloride for many species studied has been found to vary from 150·6 millimols (pollack) to 172·6 millimols (conger) per litre. Supplementary chloride data upon specimens removed from the Naples aquarium and upon *Orthagoriscus mola* (from a large tunny-net) are reported.

It has further been demonstrated that both plasma chloride and delta are as a rule considerably elevated in fishes caught on a long line or by net, and in fishes bled only after a delay and rough handling. It is emphasized that this represents a serious source of error in studies upon normal osmotic pressure relationships and upon the relative tonicity of the body fluids in marine teleosts.

Certain of the Labridæ have been found to contain in their plasma a blue or green pigment.

A. L. G.

Renal Function in Marine Teleosts. I. Urine Flow and Urinary Chloride.

By Allan L. Grafflin.

Biol. Bulletin, Vol. LXIX, 1935, *pp.* 391–402.

The present observations upon urine flow and urinary chloride in marine teleosts have led to the following conclusions: (1) that freshly caught sculpins and flounders, under fairly ideal and constant experimental conditions, show a rather wide variation in the rate of urine flow and the urinary chloride concentration; (2) that there is no direct relationship between the rate of urine flow and the urinary chloride concentration. When examined in conjunction with previously recorded observations, particularly those of Pitts (1934), the present data apparently justify a third conclusion: (3) that while all marine teleosts apparently have the *capacity* to excrete a chloride-free urine, and in their normal habitat do so in the majority of instances, they not infrequently excrete variable, and at times considerable, amounts of chloride in the urine under normal physiological conditions.

A. L. G.

The Locomotory Rhythm of the Dogfish, *Scyllium canicula.*

By J. Gray and A. Sand.

J. Exper. Biol., Vol. XIII, 1936, *pp.* 200–209.

To determine whether the muscular co-ordination of the swimming rhythm depends on proprioceptor reflexes, or whether it is entirely central in origin, cinematographic records were made of a dogfish in which the somatic muscles were denervated over a region of twelve segments at the level of the anterior dorsal fin. The fish was clamped by the denervated region. Analysis of the record shows that during normal swimming and also when the fish is excited by tactile and nociceptive stimuli, the movements of the anterior and posterior trunk regions are strictly co-ordinated. The spinal preparation, similarly treated, gave the same result. When, however, the spinal cord is transected at two levels, behind the medulla and at the level of the anterior dorsal fin, the anterior and posterior portions of the preparation exhibit independent rhythms, and the excitation of one portion by peripheral stimulation leaves the rhythm of the other portion unchanged. These observations furnish clear evidence that the locomotory rhythm of an intact or spinal dogfish is determined by the intrinsic activity of the spinal cord without the participation of proprioceptor arcs.

A. S.

Spinal Reflexes of the Dogfish, *Scyllium canicula.*

By J. Gray and A. Sand.

J. Exper. Biol., Vol. XIII, 1936, *pp.* 210–218.

When the spinal cord of the dogfish is transected behind the medulla, a preparation is obtained which survives in the laboratory tanks for many weeks. The spinal dogfish does not maintain its equilibrium, and is unable to feed, but its respiration is normal, and its reflex activity vigorous. The fish displays a persistent undulatory rhythm which is maintained as long as the animal survives. Since the motor paths from the head to the trunk are severed it is possible to anchor the fish by its snout in a shallow tank, and record the undulatory rhythm and the reflex responses of the trunk on a kymograph or cinematographically. When undisturbed the spinal fish maintains a spontaneous rhythm at a frequency of about 40 per minute, and of uniform amplitude. By means of appropriate mechanical stimulation of the trunk or fins the rhythm may be accelerated, augmented, or arrested. Acceleration is induced by light tactile stimulation of the trunk or fins. Increase in amplitude and reduction in frequency of the waves is achieved by strong pressure applied to the tail, while pressure applied to the body by means of a clamp brings about an arrest of the rhythm, which emerges again when the clamp is removed.

A. S.

Studies on Living Protoplasm. I. Streaming Movements in the Protoplasm of the Egg of *Sabellaria alveolata* (L.).

By J. E. Harris.

Journn. Exp. Biol., Vol. XII, 1935, *pp.* 65–79.

The movements of the granules in centrifuged (unfertilised) eggs of Sabellaria have been found by cinematographic observations to be determined largely by powerful currents in the protoplasm. These produce displacements of the granules far in excess of those which would be expected if they were merely particles undergoing random Brownian movement. The extent and magnitude of the streaming movements were estimated. In addition to a fairly rapid streaming over the whole egg at the rate of 30 per minute, there is also a number of smaller localised vortices described at a much slower speed (1 to 4 per minute). The general streaming movements are similar in appearance to the phenomenon of endoplasmic cyclosis.

Superimposed upon this directed motion there is a typical random movement of the particles (Brownian movement). The extent of this can be roughly estimated, and leads to a calculated value of 0·2 C.G.S. units for the hyaloplasmic viscosity, a result in fair agreement with values obtained by independent methods. On the basis of these observations it is suggested that the reactions of living protoplasm are chiefly confined to the optically structureless hyaloplasm.

J. E. H.

Note concerning a Measuring Plankton-Net.

By H. W. Harvey.

J. Cons. int. Expl. Mer., Vol. X, 1935, *pp.* 179–184.

A meter is described which measures the volume of water which has passed through a silk net which may be either towed or lowered and raised vertically.

The catch of phytoplankton, from a volume of water which has been measured by the meter, may be assessed from its content of yellow-green pigments, which readily dissolve in acetone.

A rapid method of measuring the pigment content of the catch in terms of arbitrary units of plant pigment is described. The arbitrary unit is related to numbers of two species of diatoms.

H. W. H.

The Pigmentary Effector System. Part VII. The Chromatic Function in Elasmobranch Fishes.

By L. Hogben.

Proc. Roy. Soc., London, B, CXX, 1936, *pp.* 142–158.

The pigmentary effector system of the integument in Elasmobranchs consists of dermal xanthophores, dermal melanophores, and epidermal melanophores.

Two species of *Scyllium* (*catulus* and *canicula*), *Rhina squatina* and two species of *Raia* (*maculata* and *brachiura*) exhibit contraction of all three types when kept in a container with white sides, and expansion when kept in one with black sides. The " background " response, which is macroscopically striking in *Rhina squatina* and *Raia brachiura*, but not so in the two species of Scyllium, is visually controlled.

The background response develops gradually and requires several days to reach its maximum. Some species of Elasmobranchs, e.g. *Raia clavata*, like the black axolotl, do not exhibit a pronounced white background response.

Within twenty-four hours after operation, total removal of the pituitary gland in all the species mentioned results in complete pallor, which persists till death. The operation can be carried out without any interference with swimming movements or other evident signs of disturbance or damage to the C.N.S., and the fish will survive at least two months.

The same result follows removal of the neuro-intermediate lobe with or without the pars ventralis.

Removal of the pars ventralis alone does not abolish the white or black background response.

Posterior lobe extracts free of pressor and oxytocic activity induce complete expansion of Elasmobranch pigment cells.

Removal of the anterior lobe alone appears to abolish the white background response. The indefinite demarcation of this lobe may be the explanation of partial recovery which ensued in one case.

L. H.

Über die Determination im Verlaufe der Eiachse bei Seeigeln.

By Sven Hörstadius.

Pubbl. Stazione Zoologica, Naples, Vol. 14, 1935, *pp.* 251–479.

These investigations were carried out at the zoological stations of Naples, Roscoff, and Plymouth. There is one animal and one vegetative gradient in the sea-urchin egg (Runnström). In this paper, first the normal gastrulation has been studied; then these gradients have been analysed, by isolating different layers of the egg and by adding them to each other in different ways. We can follow, how some properties decrease from the animal towards the vegetative pole, and *vice versa.* In a fragment the regulation takes place in such a way that the gradients become more concentrated at the poles. The interactions between the different parts of the eggs are studied. The most vegetative material can induce endoderm formation in animal, presumptive ectoderm, material. On the other hand, the animal forces can suppress the vegetative ones, if the former are too greatly in excess. The differentiation of a harmonic larva is not due to the absolute amount of animal and vegetative material present, but to the relative amounts: there must be a certain equilibrium between them for typical differentiation to proceed. The most vegetative material (the micromeres), when implanted in the side of an entire egg, induces a supplementary archenteron, and forms a supplementary skeleton. When implanted at the animal pole of an animal half, the micromeres may cause the reversal of the polarity of the egg-axis.

S. H.

Curarization in the Neuro-muscular System of Crabs.

By Bernhard Katz.

J. Physiol., Vol. LXXXVI, 1936, *pp.* 14P.–15P.

The neuro-muscular system of *Carcinus maenas* is unaffected by curare, while Mg, in relatively low concentrations, has a "curarizing" action. Normally, the majority of neuro-muscular junctions in crabs do not transmit a single nerve impulse; the muscle fibres need batteries of nerve impulses before responding. Lapicque's theory of curarization is discussed; the curarizing effect of Mg in crabs cannot be interpreted from the standpoint of this theory.

B. K.

The Physiology of Contractile Vacuoles. I. Osmotic Relations.

By J. A. Kitching.

J. Exper. Biol., Vol. XI, 1934, *pp.* 364–381.

Marine Peritrich Ciliates showed an increase in body volume, and a great increase in the rate of output of fluid from the contractile vacuole, when they were treated with hypotonic sea water. The greatest increase was about ×70, in 10% sea-water. On a return of the organism to 100% sea-water the rate of vacuolar output returned approximately to its original value, and the body shrank to its original size or less. Fresh-water Peritricha showed a decrease in rate of vacuolar output when subjected to mixtures of fresh-water and sea-water. Theoretical reasons are advanced in favour of the view that the osmotic concentration of the vacuolar fluid is very low, in which case the contractile vacuole may be regarded as a mechanism of osmotic control. It is suggested that marine and estuarine Peritricha only maintain their internal osmotic pressure significantly higher than that of the external medium when in hypotonic sea water. The rate of vacuolar output of marine Peritricha in 100% sea water is very low, and it is unlikely that it maintains any great difference of osmotic pressure between the internal and the external media.

J. A. K.

The Physiology of Conractile Vacuoles. II. The Control of Body Volume in Marine Peritricha.

By J. A. Kitching.

J. Exper. Biol., Vol. XIII, 1936, *pp.* 11–27.

From experiments in which a large part of the salts of sea-water were replaced by an osmotically equivalent amount of glycerol, urea, or cane sugar, it is concluded that the body surface of marine Peritricha is relatively impermeable both to these substances and to the neutral salts of sea water. Cyanide and sulphide in very low concentrations (the pH being carefully controlled) were found to inhibit the secretory activity of contractile vacuoles, while alcohols and urethane were only effective in much higher concentrations. It is possible that there is a direct connexion between vacuolar activity and respiration. When the contractile vacuole of a marine Peritrich which was in dilute sea-water was stopped by the addition of cyanide, there was a further increase in body volume. This further increase was greater the more dilute was the sea-water, down to 10%, and may be regarded as a measure of the body volume control effected by the contractile vacuole. Return of the organism to dilute sea water of the same concentration but without cyanide led to rapid recovery and great activity of the contractile vacuole, which was accompanied by a decrease of body volume to a value somewhat less than it had been before cyanide treatment. The extent of this body volume decrease was quantitatively in accordance with expectation having regard to the known rate of vacuolar output. The permeability of the body surface to water was estimated as 0·05–0·10 cubic micra per square micron per atmosphere per minute.

J. A. K.

The Importance of Larval Mollusca in the Plankton.

By M. V. Lebour.

J. Cons. int. Explor. Mer., Vol. VIII, 1933, *pp.* 335–343.

A survey of mollusca in the plankton based mainly on the work on gastropod larvæ carried on during the last few years at Plymouth. It is shown that molluscan larvæ are extremely important economically, serving as food for many animals including fishes. Some are always to be found in the plankton, different species in different seasons. The gastropod larvæ from the outside water are usually larger than the shore forms and very well adapted to a planktonic life, having a large velum and long larval stage.

M. V. L.

Larval Crustacea (Decapoda and Stomatopoda) Expedition S.A.R. Prince Léopold of Belgium, Duke of Brabant, to the Extreme East (1932).

By M. V. Lebour.

Bull. Mus. Roy. d'Hist. Nat. Belgique, T. X, No. 8, 1934.

Some little-known larvæ from the Philippine Islands are briefly described, although only approximately placed in their systematic positions, the adults to which they belong being not as yet known. The larvæ include pagurids, brachyurids and one stomatopod.

M. V. L.

Stomatopod Larvae.

By M. V. Lebour.

Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises de LL.AA.RR. le Prince et la Princesse Léopold de Belgique, Vol. III, Fasc. 16, 1934, *pp.* 9–17.

Four specimens of stomatopod larvæ are recorded, one being a post-larval stage almost certainly belonging to *Gonodactylus chiagra*, the others being Squilla larvæ the adults of which are not known.

M. V. L.

The Life-History of *Dromia vulgaris*.

By M. V. Lebour.

Proc. Zool. Soc., London, 1934, *pp.* 241–249.

An account of the larval stages of *Dromia vulgaris*, including pre-zoea, first, second and fifth zoeæ and megalopa. The pre-zoea was hatched from the egg and the first and second zoeæ obtained from these. The fifth (last) zoea was found in the Plymouth plankton in September 1933 (two specimens, each on a separate occasion), and the megalopa was obtained from one of these. It is very unusual to find these larvæ at Plymouth although the adults are occasionally brought in. The larval characters show clearly that Dromia should not be included in the Brachyura, but is much more closely related to the Anomura having affinities with the Thalassinidea, although it probably should not be included in either of these last groups but placed separately and not in the direct line of descent from the Brachyura.

M. V. L.

The Echinospira Larvæ (Mollusca) of Plymouth.

By M. V. Lebour.

Proc. Zool. Soc., London, 1935, *pp.* 163–174.

An account of the larvæ of two species of Lamellaria, two of Trivia, one Erato and one Velutina from Plymouth. All these have Echinospira larvæ, the transparent accessory shells serving as floats. Velutina has the Echinospira shell gelatinous, the two species of Trivia and Erato differing from the Lamellariidæ in the form of the Echinospira but showing a close relationship. It is probable that their natural position is nearer to Lamellaria than to the true Cypraeas.

M. V. L.

Notes on the Plymouth Species of Spirontocaris (Crustacea).

By M. V. Lebour.

Proc. Zool. Soc., London, 1936, *pp.* 89–104.

An account of a new species of Spirontocaris (*S. occulta*) compared with *S. cranchii*. The two have probably been confused hitherto as they are outwardly much alike. *S. cranchii* differs from *S. occulta* in the absence of mandibular palp and in having six segments in the carpus of the second leg instead of seven. The larvæ of the two species also differ and are easily separated. Both were hatched from the egg and later stages were obtained from the plankton. Post-larvæ and young stages were reared from the last larvæ. The mandibular palp in *S. occulta* appeared late and was absent altogether from the first young stage, showing probably the dwindling of a useless organ. A comparison with the genus Thor is made.

M. V. L.

A Third List of Parasitic Copepoda of Plymouth with Notes.

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXVI, 1934, *pp.* 112–113.

In addition to new local species, an account and figures are given of the erosion made by *Lernæopoda bidiscalis* on the clasper of the tope.

W. H. L.-S.

Epibrachiella impudica (Nordmann) (Copepoda).

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXVII, 1935, *pp.* 101–106.

An account of the animal and appendages of both sexes. Amendations of Wilson and Nordmann in the male; confirmation of the work of Harrison Matthews. New reasons for erecting the genus Epibrachiella. Characters of the female overlooked by all but Brian. Discrepancies between Scott's diagnosis and his own specimens in the British Museum. Differences between young and adult forms.

W. H. L.-S.

Some New and Rare Lernæidæ (Copepoda) from Plymouth.

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXVII, 1935, *pp.* 107–110.

Record of *Hæmobaphoides ambiguus.* Erection of the new genus *Saucissona*, with a description of a new species, and to include Scott's *S.* [*Lernæa*] *lumpi.* Description of a new species *Lernæocera mulli.*

W. H. L.-S.

Anchistrotos laqueus n. sp. A Parasitic Copepod of *Serranus cabrilla.*

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXVII, 1935, *pp.* 266–269.

Diagnosis of Brian's genus Anchistrotos. Description of a new species with appendages. A comparison with *Bomolochus bellones.*

W. H. L.-S.

Two Copepods (Lernæenicus) parasitic on Clupea.

By W. H. Leigh-Sharpe.

Parasitology, Vol. XXVII, 1935, *pp.* 270–275.

Descriptions of *L. spratta* and *L. encrasicholi* with appendages. Occurrence at Plymouth and elsewhere. First record of the eye in British species. Presence of two pairs of maxillæ (first pair absent in American species).

W. H. L.-S.

The Respiratory Rate of *Gammarus chevreuxi* in Relation to Differences in Salinity.

By Otto Löwenstein.

J. exp. Biol., Vol. XII, 1935, *pp.* 217–221.

The brackish water amphipod *Gammarus chevreuxi* is found in ditches in a salt marsh at the mouth of the River Plym. It lives in water, the salt content of which varies continually owing to tidal flooding from the estuary and to the inflow of fresh water and rain. In connection with the question of osmoregulation the oxygen consumption of this apparently euryhaline animal was measured in 25 per cent sea-water and after transfer into 100 per cent sea-water. The respiratory rate was found to be approximately 20 per cent lower in sea-water than in 25 per cent sea-water which is a concentration occurring in the natural habitat. Anæsthetized animals showed the same percentage decrease as unanæsthetized animals.

The change in oxygen consumption takes place immediately after the transfer and remains constant thereafter. It is completely reversible.

A comparison with the unanæsthetized respiratory rates of the related fresh-water species. *G. pulex* and marine *G. marinus* shows that the rate of oxygen consumption of the brackish-water form *G. chevreuxi* in 25 per cent sea-water lies between the two others.

O. L.

The Significance of the Spontaneous Discharge from the Horizontal Ampulla of the Dogfish.

By Otto Löwenstein and A. Sand.

J. Physiol., Vol. LXXXVI, 1936, *pp.* 43P.–44P.

The activity of the horizontal ampulla during rotation in the horizontal plane was investigated by obtaining oscillographic records of the action potentials in the branch of the eighth nerve supplying this ampulla. The ampullary organ maintains a spontaneous discharge of impulses in the absence of rotatory stimulation. During ipsilateral rotation the discharge is increased, and when rotation is stopped the discharge returns again to its resting level. Contralateral rotation abolishes the spontaneous discharge, but on stopping a prolonged outburst of after-discharge occurs. By virtue of its spontaneous activity the ampulla is able to discriminate left and right angular acceleration. The two opposite ampullæ work antagonistically and therefore the quantitative effect of rotation is greater at the centre than at the receptor on either side. The observations furnish an explanation of reflex eye-muscle responses which have been found to occur in unilaterally operated fishes. A. S.

The Swimming and Feeding of Certain Calanoid Copepods.

By A. G. Lowndes.

Proc. Zool. Soc., London, 1935, *pp.* 687–715.

In recent times there has been a marked tendency to over-stress filter-feeding among crustacea in general and it has been maintained by several writers that the feeding of the Calanoid copepods in particular is automatic and non-selective. The animals are supposed to feed automatically as they swim.

Nine common species were examined critically. Limb-movement being investigated chiefly by ultra-rapid cinema photomicrography while the nature of the food was ascertained chiefly by an examination of the gut-contents.

Work on the gut-contents had been done by well-known workers both at Plymouth and Millport and it is somewhat surprising that this work has been disregarded.

Three of the species investigated occurred in fresh water, and it was definitely established that *Diaptomus gracilis*, though living in ponds abundantly supplied with floating algæ, was yet descending periodically and feeding on Desmids growing on the bottom of the pond.

Calanus finmarchicus itself feeds in a variety of ways. For long periods it does not feed at all. It is suggested that the so-called feeding currents set up by the Calanoid copepods are really respiratory in effect.

The female of *Euchæta norvegica* feed almost entirely on *Calanus finmarchicus.*

One important point must be taken into consideration. Gurney has recently re-classified the Calanoid copepods and regards the Centropagina and not the Calanina as the more primitive group, and the former group with Centropages itself are certainly raptorial. Thus even if the Calanina were exclusively filter-feeders there is little reason for regarding the process as being the more primitive one. A. G. L.

Some Measurements of the Brightness of Various Parts of the Sky by means of a Rectifier Photo-electric Cell.

By H. H. Poole and W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1933, *Vol.* **21**, *pp.* 1–8.

A selenium cell was used which gives results not differing greatly from the visual scale. It was mounted in place of the mirror in an old reflecting telescope. Two figures show the variation of the brightness of the sky with altitude for various azimuths relative to that of the sun, under different meteorological conditions. As compared with a very clear blue sky the effect of haze, and to a greater extent that of light cloud, is to (*a*) increase the illumination from all parts of the sky above about 10° altitude, (*b*) increase the relative proportion of high-angle light, and (*c*) increase the relative brightness of the sector containing the sun, and hence greatly to increase V_d the vertical illumination from the whole sky. For a perfectly uniform sky the ratio V_d/I_d is 0·5, where I_d is the total diffuse illumination. With a clear sky V_d/I_d was rather less than this, while the reverse was true with a cloudy sky. Except near the sun the sky illumination on bright summer days was about 1–4 metre candles (lux) per square degree. White clouds may give 7 lux, about 10 times the brightness of a deep blue sky, or 3·5 times the brightness of a candle flame which is about 2 lux per square degree.

W. R. G. A.

Measurement of the Current Generated by a Rectifier Photo-electric Cell.

By H. H. Poole and W. R. G. Atkins.

Nature, Vol. CXXXIV, 1934, *p.* 810.

The Measurement of the Current Generated by Rectifier Photo-Cells.

By H. H. Poole and W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1934, *Vol.* **21**, *pp.* 133–139.

A description is given of a modified form of the circuit described by Campbell and Freeth. The modification consists in the deduction of the current from a potentiometer setting and the resistance in the circuit, instead of its direct measurement. For this use was made of the potentiometer-amplifier-telephone null-point apparatus devised for work at sea. This enables accurate measurements to be made of a range of illuminations from a small fraction of a metre-candle up to full sunlight while preserving all the advantages of a zero-resistance measuring instrument. It is especially suitable for work at sea.

W. R. G. A.

The Standardization of Photo-electric Cells for the Measurement of Visible Light.

By H. H. Poole and W. R. G. Atkins.

Phil. Trans. Roy. Soc., London, A, Vol. CCXXXV, 1935, *pp.* 1–27.

Constants relating to nineteen vacuum emission and rectifier cells have been tabulated. As light sources the following were used: open solid carbon arc; vacuum sub-standard filament lamp at 2360° K; artificial "mean noon sunlight" derived from the latter by interposing special liquid filters. The cells were also compared in mixed daylight. For sodium and potassium cells only the arc gives a scale of values reasonably close to the visual; this method is suitable for other emission cells and for rectifier cells. Selenium rectifier cells have colour sensitivities close enough to that of the eye to allow of the use of the mean noon sunlight source. Close agreement is given by the selenium cell standardized in artificial sunlight and the potassium cell in arc light, when both are used to measure bright mixed daylight.

Vacuum potassium and sodium cells maintained their sensitivity constant for over five years; a selenium cell has remained constant for over a year. The sodium and potassium cells maintained a rectilinear proportionality between illumination and current up to full summer daylight. The curvature of the illumination/current characteristic of rectifier cells is important and must be allowed for.

W. R. G. A.

Observations on the Embryonic and Larval Development in Sacculina (Rhizocephala) in Changed Osmotic Conditions of Medium.

By M. Ramult.

Bull. Int. Acad. Pol. Sci. et Lettr. Cracovie, 1935, *pp.* 87–109.

The eggs and larvæ of *Sacculina carcini* were investigated as to the ability to develop in hypo- and hypertonic sea-water and sodium-chloride solutions. The eggs of the above-named species, which pass as a rule their embryonic development in the maternal mantle cavity, were artificially extracted out of the latter just after having passed from the ovary (before entering the cleavage). They developed normally in such conditions till the Nauplius-stage not only in normal sea-water but also in sea-water solutions of the concentration from 2·45 per cent to about 4·1 per cent of mineral constituents. The 4-blastomeres stage proved to be more resistant to the osmotic and chemical changes of the outer medium than the freshly laid egg, as it could develop till the Nauplius stage in 1·75 per cent sea-water. In pure NaCl solutions the freshly laid and artificially extracted Sacculina eggs can develop in the concentrations from 2·45 per cent to about 4·1 per cent but only to the 4-cell stage. The Nauplius larvæ can pass the metamorphosis till the Cypris stage in hypotonic sea-water solutions from 2·45 per cent of mineral constituents upwards.

The resistance power in the eggs and larvæ of *S. carcini* to hypotonicity seems to be in accordance with the resistance power of the host of this parasite, i.e. *Carcinus maenas*, which lives in normal sea-water as well as in hypotonic brackish waters of estuaries and of western part of Baltic Sea.

M. R.

The Strength-duration Curves of two Non-Medullated Nerves.

The Excitation of Medullated and Non-Medullated Nerves by Currents of Short Duration.

By H. Rosenberg.

J. Physiol., Vol. LXXXIII, 1934, *pp.* 23P.–24P., *Vol. LXXXIV*, 1935, *pp.* 50–69.

These investigations concern comparative measurements of excitability in different types of nerves. Strength-duration curves of medullated amphibian and mammalian nerves, and of non-medullated nerves of invertebrates, were recorded for semi-maximal electrical responses of the nerves stimulated by single condenser discharges of graded voltage and discharge time. Ballistic deflections of a moving-magnet galvanometer were used as index of response. The main result is that below a certain discharge time, varying in different types of nerves and under different conditions, the minimum quantity of electricity required for excitation is constant. This quantity is of the order of 10^{-9} coulomb in medullated nerves (sciatic, ulnar and phrenic of frog, cat and dog) and of 10^{-7} to 10^{-6} coulomb in non-medullated nerves (limb nerve of Maia and fin nerve of Sepia). The characteristic time which corresponds with the minimum of energy is about the same for frog's and cat's sciatics at the same temperature, but twice as great in the dog's phrenic where the fibre diameter is smaller. In Sepia nerve this time is about 1·4 msec., in Maia nerve about 10 msec. These values concern electrode distances of 10 to 15 mm. When the electrode distance is diminished from 15 to 3 mm. in non-medullated nerves, the characteristic time, as well as the chronaxie, decrease by about 25 per cent. The minimum quantity is distinctly greater for short than for long distances, and the difference increases with increase of discharge time.

H. R.

Electrotonus in the Fin Nerve of Sepia.

By J. Yule Bogue, H. Rosenberg and J. Z. Young.

J. Physiol., Vol. LXXXVI, 1936, *pp.* 6P.–7P.

In view of the importance of electrotonus in the excitation process electrotonic potential changes in the main trunk of the non-medullated fin nerve of Sepia were recorded by means of a direct coupled amplifier and a mechanical oscillograph. The distances between the distal leading to and the proximal leading off electrodes were 2·5 to 8 mm. At short distance the electrotonus showed a comparatively small quick component at make of the polarizing current and rose then slowly to a certain level. The duration of this rise was of the order of 0·05 sec. at 2·5 mm. distance. After break there was a similar rapid drop which was also followed by a gradual decline of a similar total duration as that of the rise. Apparently the phenomena were of the same order in an- and catelectrotonus. But owing to the strength of the polarizing current, the catelectrotonic curve was distorted by a superimposed action-potential wave while this interference was negligible in the anelectrotonic curve because of the anode block. (Measurements proved that stimulation occurred at the cathode.) With increase of the distance the quick component vanished and the rate of rise of the slow component decreased. At a medium distance half the maximum was attained about fifty times slower than in the frog's sciatic.

H. R.

The Trematode Parasites of *Turritella communis* Lmk. from Plymouth and Naples.

By Miriam Rothschild.

Parasitology, Vol. XXVII, 1935, *pp.* 152–170.

Six new species of closely related cercariæ of the Rhodometopa group are found in *Turritella communis* from Plymouth (20 fathoms) and Naples. Their outstanding morphological characters are (*a*) the elaborate excretory system (122 or 144 flame cells) in which the much-branched excretory vesicle itself grows forward after the development of the main collecting tubules, (*b*) the highly specialized longitudinal and lateral fin folds of the tail, (*c*) the pink pigment often present anteriorly. The excretory granules are an important specific character. Development occurs in redia-like sporocysts which multiply by fission and budding. They possess salivary glands and a fifth (most internal) layer to the body wall.

The cercariæ swim upwards on emerging. In a tube 30 feet high *C. pythionike* reaches the top in five hours. As the life of the cercariæ is fifty hours the intermediate host may be found even among the plankton. *C. doricha* only rises about 10–15 feet.

Infection experiments with thirty-six species of animals from the Turritella grounds proved negative. (*C. doricha* made abortive attempts to penetrate the fins of *Pleuronectes platessa.*) Three hundred and fifty of these animals were dissected, but no metacercariæ were found pertaining to these cercariæ.

M. R.

New Developments in *Gammarus chevreuxi*, Sexton.

By E. W. Sexton and A. R. Clark.

Nature, Vol. CXXXIII, 1934, *p.* 27.

For many years the wild *G. chevreuxi* found in the salt marsh, Chelson Meadow, were considered a homogeneous black-eyed population. More recently, conditions have changed in the draining ditches which they inhabit, affecting the depth, salinity and temperature. Great variability appeared and it soon became clear that heterozygosity must exist in the stock, although so far, only black-eyed specimens had ever been found.

Now, for the first time, direct evidence has been obtained, in the F_1 from a female which had mated and laid eggs in the wild. That it was heterozygous and had mated with a heterozygous male, was shown by its brood, which consisted of nine black-eyed young to two red-eyed recessives.

E. W. S.

First Appearance of Red-eye in the Wild *Gammarus chevreuxi*, Sexton.

By E. W. Sexton, A. R. Clark and G. M. Spooner.

Nature, Vol. CXXXVI, 1935, *p.* 836.

Heterozygosity in the wild Gammarus population was proved for the first time in 1934 by the appearance of red-eyed recessives in the F_1 from a pair newly brought in. In 1935 the final proof was obtained from an October dredging, which consisted of one red-eyed amongst two thousand black-eyed animals.

E. W. S.

The Early Development of the Nemertean *Cephalothrix rufifrons.*

By J. E. Smith.

Quart. J. Micr. Sci., Vol. LXXVII, 1935, *pp.* 335–381.

A description is given of fertilization, early cleavage, gastrulation and early organogeny of the nemertean *Cephalothrix rufifrons.* A direct development is followed in which the "anlagen" appear and develop without metamorphic changes. In this respect, the larva of the Palæonemertini, as represented by Cephalothrix, is to be regarded as a less-specialized form than the Pilidium or Desor larva of other anoplous nemerteans.

Although the enoplous nemerteans also have a direct development the developmental processes exhibit a marked telescoping in that all the organ "anlagen" are represented in the blastula or gastrula. This latter type of direct development is considered to be even less closely related to the direct development of the Anopla than is the development through the Pilidium or larva of Desor.

The unspecialized larva of Cephalothrix is represented as a primitive form reminiscent, in many respects, of the platyhelminth condition, particularly in the absence, until late in development, of an anus and in the endodermal nature of the hind-gut.

J. E. S.

The Measurement of "Accommodation" in Nerve.

By D. Y. Solandt.

Proc. Roy. Soc., London, B, CXIX, 1936, *pp.* 355–379.

Experiments are outlined by which Hill's (1935 and 1936) theory concerning the time-constant of "accommodation" in the electrical excitation of nerve is verified. The predicted linear relation between relative threshold and time-constant of exponential rise of current was found for certain motor nerves of frogs, fishes, crabs, lobsters and man. The slope of this line has been shown by Hill to be the reciprocal of λ, the time-constant of "accommodation." Measures of λ were thus obtained on a variety of nerves under various conditions. The sciatic nerves of normal winter frogs (*Rana esculenta* and *Rana temporaria*) showed an average value of $\lambda=35$ msec. at room temperature. Fish had somewhat larger values of λ, averaging between 11 and 20 msec. Crabs and lobsters had values of λ between 800 and 7690 msec. The average value of λ for the human ulnar nerve was 58 msec. Increasing the concentration of calcium or potassium around a frog's nerve either by injecting the chloride into the animal, or by adding it to the Ringer's solution used to soak the preparation was found to lower λ. In the case of normal winter frogs injected with more than 100 mg. of $CaCl_2$, λ was as small as 6 msec. Magnesium acted similarly but more slowly, while strontium and barium also had the same effect but to a lesser degree. Increasing the ionized calcium concentration in the environment of a crab's nerve, or of the human ulnar nerve, was found to lower λ. Decreasing the calcium ion concentration in the environment of frog's sciatic nerve was found to raise λ till, in the absence of calcium, it approached infinity. No other treatment (except a lowering of temperature) was found by which λ could be increased. Decreasing the calcium-ion concentration in man, by the ingestion of alkali, increased the value of λ. The effect of calcium on λ is much greater than on k. This shows that the time-constants of " accommodation " and of " excitation " are independent.

D. Y. S.

Development of *Patella vulgata.*

By F. G. Walton Smith.

Phil. Trans. Roy. Soc., B, CCXXV, 1935, *pp.* 95–125.

An account is given of breeding habits and methods of rearing the larva together with a brief explanation of the technique employed in embedding and sectioning the various stages of development. Development is described from early stages of segmentation up to the stage at which the post-larva casts off the larval shell and becomes a miniature limpet. Formation of the mesodermal rudiments and their subsequent transformation into kidney and pericardium rudiments is explained, and the origin and development of heart, nervous system, alimentary canal and liver, sensory organs, radula sac, and pedal glands are described. A suggestion is advanced as to the mechanism responsible for larval torsion, and the new points briefly summarized.

F. G. W. S.

Some Remarks on North Atlantic Non-Pelagic Polystilifera.

By G. Stiasny-Wijnhoff.

Quart. J. Micr. Sci., Vol. LXXVII, 1934, *pp.* 167–190.

Description of three Polystilifera Reptantia: *Uniporus borealis* (Punnett) from Davis Strait, *Hubrechtonemertes lankasteri* (Hubrecht) from the American waters and *Punnettia splendida* (Keferstein) from the neighbourhood of Plymouth. The material of *Uniporus borealis* existed in the original series of Punnett, whose description needed some more extensive details of some organs, as brains and cerebral organs. *Hubrechtonemertes lankasteri* is *Drepanophorus lankasteri* of the Challenger expedition; this species was insufficiently known. To settle its relation to the other Polystilifera the original material of Hubrecht was studied.

Both these species belong to the Reptantia with atrium and with the type of cerebral organ that is characteristic of the Inæquifurcata.

Hubrechtonemertes is nearly related to *Paradrepanophorus* and not to *Uniporus*, as some authors supposed.

Punnettia splendida has been studied from material collected at the Plymouth Laboratory. McIntosh identified it with *Cerebratulus spectabilis* Quatrefages from Sicily; Hubrecht supposed it to be identical with his Mediterranean *Drepanophorus rubrostriatus* and Bürger united all these species in one. The detailed study of the Mediterranean and the English material showed that McIntosh was right when he took the Channel-material as different from Hubrecht's *rubrostriatus*. The original name of Keferstein ought to be used for the English Nemertean, that is not known from anywhere beyond the English Channel.

G. S.-W.

Vergleichende Untersuchungen über das Periphere Nerven-Muskel-System von Crustaceen.

By C. A. G. Wiersma.

Zeitschrift für vergleichende Physiologie, 19, 1933, *pp*. 349–385.

The abductor and adductor muscles of different crustaceans were studied. The adductor shows two kinds of contractions: a twitch and a slow contraction. When stimuli near the threshold of the twitch are given either no contractions results or the contraction is large (Astacus). Stronger stimuli increase the height of contraction suddenly, in step-like fashion. It is reasoned that this sudden increase is due to a repetitive discharge in the motoric nerve fibres.

Strength-duration curves for several crustaceans were determined, each having several steps. In different crustaceans different numbers of impulses seem necessary to produce the same effect, namely, the closing of the claw. The muscle action currents were recorded; for the higher steps of the twitch several tops were found. When a slow contraction occurred there always appeared a long series of tops in the action current record; these tops grow in size but diminish in frequency, though they never equal those of the twitch in height.

In the abductor both contractions may also occur, but the twitch is much more difficult to obtain.

A working hypothesis to cover the results is given.

In experiments on inhibition only the abductor could be readily inhibited.

C. A. G. W.

On the Nature and Permeability of Chitin. II. The Permeability of the Uncalcified Chitin Lining the Foregut of Homarus.

By C. M. Yonge.

Proc. Roy. Soc. London, B, Vol. CXX, 1936, *pp.* 15–41.

As shown in the first paper in this series, the integument of the Decapod Crustacea consists of a thick, underlying chitinous layer, and a thin superficial cuticle which is not chitin but contains a lipin. The former is formed by the epithelial cells, the latter by the tegumental glands.

Permeability of this membrane where, as in the foregut, it is uncalcified, is profoundly modified by the presence of the cuticle. When this is intact fatty acids penetrate much more quickly than the strong mineral acids, HCl or HNO_3, and ammonia more quickly than the strong alkalies, $NaOH$ and KOH. After removal of the lipin both acids and alkalies pass through in the order of their degree of dissociation.

The passage of chloride with divalent cations is greatly inhibited when the cuticle is intact and distinctly more in the direction cuticle to chitin than in the opposite direction. There is the same difference between the passage of $Ba(OH)_2$ and that of KOH, $NaOH$ or $LiOH$. These differences disappear after the lipin has been removed.

Glucose penetrates "fresh" membranes very slowly but rapidly after the removal of the lipin. In fresh membranes permeability is notably lowered at the iso-electric point of the cuticle and after removal of the lipin at that of the chitin. Permeability through both types of membranes is influenced by hydrogen ion concentration and also by the action of specific ions other than hydrogen.

Fat solvents penetrate fresh membranes suspended in air but only in the one direction, cuticle to chitin.

Unimpregnated chitin forms a freely permeable membrane, the presence of the cuticle converts this into a membrane with variable degrees of permeability, which has certain properties analogous with those of the living cell membrane.

The significance of both chitin and cuticle in the life of the animals possessing them is discussed.

C. M. Y.

Book Notice.

The Algae and their Life Relations.

Fundamentals of Phycology. By Josephine E. Tilden. Univ. of Minnesota Press, 1935. Oxford Univ. Press, 22s. 6d. net.

The book is primarily a text for advanced students in botany. It is designed as a guide to the student and a reference book for investigators. The first three chapters deal with the phylogeny of the algæ, their distribution in time and space and a classification based on evolutionary development with special reference to pigmentation and food reserves. These are highly speculative and statements are made concerning the probable illumination over the earth's surface in past ages which are much too definite to be acceptable.

The next five chapters constitute the bulk of the book and deal with the classification and morphology of the algal groups. This part is well done, and the illustrations are clear. A feature of the book is the introduction of numerous diagrams showing the alternation of generations and comparisons between those of algæ and higher plants. The ninth chapter deals, quite inadequately, with algal control, and the tenth has some interesting observations on the algal food of animals, but it appears to the reviewer that the importance of the plankton has been greatly underestimated. Chapter eleven may be dismissed as journalistic propaganda for marine algæ as "our richest source of vitamins." There is a useful appendix on the drawing of algæ for publication and a valuable bibliography of over 700 titles.

W. R. G. Atkins.

Marine Biological Association of the United Kingdom.

Report of the Council for 1935.

The Council and Officers.

Four meetings of the Council have been held during the year in the Rooms of the Royal Society, London. The average attendance was fourteen. The thanks of the Association are due to the President and Council of the Royal Society for allowing their rooms to be used. A Committee of the Council consisting of ten members and presided over by the Chairman of Council, Prof. E. W. MacBride, F.R.S., visited and inspected the Plymouth Laboratory on April 6th.

The Council has to record with regret the death of Mr. T. H. Riches, who was a member of Council from 1920 to 1926 and had since 1889 taken a great interest in the Plymouth Laboratory, where he carried out his own research work from that date until 1896. He became a Founder of the Association in 1900 and for the rest of his life gave most valuable help in raising money for special funds for enlarging the Laboratory buildings and similar purposes, in addition to making substantial contributions to them himself.

The Plymouth Laboratory.

Repairs and painting necessary to maintain the Laboratory buildings and fittings in good condition have been carried out. It was found necessary to renew part of the electric light wiring in the main building, and to replace the aerial cable leading to the Easter House. The ejector previously used for pumping water from the sea into the main reservoirs has been replaced by a centrifugal pump supplied by the Pulsometer Company and driven by an electric motor. It is now possible to fill an empty reservoir to its working capacity of 50,000 gallons in about three and a half hours.

The Aquarium.

The number of visitors to the Aquarium has again increased, including many parties of school children in charge of their own teachers. A few of these parties have come from towns distant from Plymouth. In addition many fishermen have from time to time paid visits and have expressed their interest and appreciation.

The tanks have been exceptionally well stocked throughout the year. Among the more unusual exhibits may be mentioned one specimen of *Balistes capriscus*, three young *Lophius piscatorius*, several *Pagellus centrodontus*, and a fine shoal of young *Caranx trachurus*.

An improved circulation to the smallest tanks has been arranged and various minor alterations carried out.

The Ship and Motor-Boat.

The steam-drifter "Salpa" and the motor-boat "Gammarus" have worked continuously throughout the year, except for the short periods occupied by the normal surveys and refits which have been carried out as usual, most of the work being done by the crews. Both boats are in good order. In August, 1933, the makers fitted new cylinders into the 6 h.p. engine of the "Gammarus" free of charge, as the old ones had been causing trouble through abnormal wear. This engine has since worked satisfactorily, but the new cylinders are already showing such considerable wear that further trouble from this source will probably arise in the near future. The makers of the engine have been communicated with, but can offer no satisfactory explanation except to state that cylinder wear has become more evident in all engines as the compression ratios have been raised, and that there is great variation in the performances of different engines of the same make, the causes of which are not as yet understood.

The Staff.

Mr. E. Ford has been appointed by the Council Assistant-Director of the Plymouth Laboratory, and commenced his new duties at the beginning of April.

Dr. A. Sand, Lecturer in the Zoological Department of the University of Cape Town, has been appointed Physiologist at the Plymouth Laboratory in succession to Dr. L. E. Bayliss. Dr. Sand took up his post in the spring.

Mr. G. I. Crawford, who had been Student Probationer since April, 1934, left Plymouth in October, 1935, to take up a post as Assistant-Keeper in the British Museum (Natural History) at South Kensington.

Mr. P. H. T. Hartley of the Zoology Department, University College, London, has been appointed to succeed Mr. Crawford as Student Probationer, and commenced work in the middle of November.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year, a number considerably in excess of other years.

S. Alexander, London (Colour changes in fishes).
Dr. J. R. Baker, Oxford (Preservation of Anemones).
Prof. G. H. Ball, Los Angeles, Cal. (Protozoa parasites in Crustacea).
Dr. E. J. W. Barrington, Nottingham (Digestion in Amphioxus).
Dr. R. Bassindale, Manchester (Barnacle development).
Dr. Helen I. Battle, Ottawa (Physical factors in fish development).
Dr. H. W. Beams, Iowa (Cytoplasmic components in invertebrates).
Dr. C. W. Bellerby, London (Physiology of reproduction of fish).
Dr. A. M. Bidder, Cambridge (Cephalopods).
Mlle G. Bloch, Bordeaux (Microsporidia living on *Ficulina ficus*).
Dr. J. Y. Bogue, London (Correlation of the electrical responses with the histological structure of nerves).
L. R. Brightwell, Horsley (Drawings of marine animals).
Miss R. Chrzanowska, Poland (Chemico-hydrological work).
A. Cohen, Cambridge and Montreal (Ascidian development).
J. S. Colman, St. Johns, Newfoundland (Library).
L. R. Crawshay, lately Officer for Sponge Research, British Honduras (Sponges).
Prof. A. Morley Davies, London (General Zoology).
Dr. B. Dawes, London (Trematodes of marine fishes).
G. E. R. Deacon, " Discovery Investigations " (Library).
Dr. E. S. Duthie, London (Histology of gills and intestines of teleostean fishes).
D. W. Ewer, Cambridge (Bioluminescence).
C. M. Fletcher, Cambridge (Action potentials in smooth muscle).
R. R. Fowell, London (Sporozoa in *Polydora flava* and Tunicates).
Miss V. Frettar, London (Structure and function of the alimentary canal of Chiton).
Miss B. Garrard, London (Osmotic pressure of Fundulus and of Scyllium eggs).
H. C. Gilson, Cambridge (Metabolism of Diatoms).
Prof. E. S. Goodrich, Oxford (Annelids).
Dr. H. L. M. Pixell-Goodrich, Oxford (Parasitic Protozoa).
Dr. J. Gray, Cambridge (Fertilisation of Echinus. Spinal reflexes of Dogfish).
Dr. S. Gripenberg, Helsingfors, Finland (Chemistry of the sea).
Dr. F. Gross, Vienna and Berlin (Rearing of marine organisms).
D. M. Hall, Cambridge (Neuromuscular action in Metridium and in *Pecten opercularis*).
Dr. W. F. Hampton, Newfoundland (Biochemistry in relation to Fisheries).
P. H. T. Hartley, London (*Trebius caudatus*).
N. I. Hendey, London (Plankton estimation).
Prof. A. V. Hill, London (Electric excitation of non-medullated nerve. Crustacean nerves).
Prof. S. Hiller, Wilno, Poland (Influence of narcotics on development of Echinoderms. Nervous system of Bryozoa).
A. L. Hodgkin, Cambridge (Electrotonus in crab's nerves).
Prof. L. Hogben, London (Colour change in fishes).
Dr. A. G. Huntsman, Ottawa (Fisheries).
Miss P. M. Jenkin, Bristol (Correlation of diatom photosynthesis and light penetration in the sea).
Miss M. L. Johnson, Birmingham (Control of respiratory movements in Crustacea).
Dr. E. Idris Jones, London (Parasitic Trematodes in fishes).
Dr. B. Katz, London (Excitability of crab nerves and muscles).
F. Khalil, Cambridge(Comparative study of sensory lateral line nerve).

Dr. J. A. Kitching, London (Contractile vacuoles).
Mrs. J. A. Kitching, London (Digestion in Gunda).
Dr. P. C. Koller, Edinburgh (Cytological studies on Balanus and Polychætes).
Dr. and Mrs. F. R. Koumans, Leiden, Holland (Mollusca).
Miss J. Kriebel, Cambridge and Erlingen, Germany (Experimental embryology).
Dr. and Mrs. Lehnartz, Frankfurt-am-Main (Arginine phosphoric acid in lobsters, crabs and Pecten).
Dr. E. Liebmann, Tel-Aviv, Palestine (Fisheries).
Dr. H. W. Lissman, Cambridge (Function of fins in Motella).
Miss M. Lister, London (Light reaction in medusae).
Dr. O. Löwenstein, Birmingham (Physiology of the Selachian labyrinth).
A. G. Lowndes, Marlborough (Feeding mechanism of Spirontocaris).
Miss A. M. Lysaght, London and New Zealand (Larval Gastropods).
Dr. D. C. G. Mackay, Ottawa (Relative growth of *Cancer pagurus*).
Miss D. M. Mees, Rochester, N.Y. (Regeneration of Sabella).
Dr. G. B. Moment, Baltimore (Function of the polar lobe in embryology of Sabellaria).
Dr. H. B. Moore, Port Erin (Quantitative studies on shore fauna).
Miss L. B. Moore, Auckland, N.Z. (General Zoology).
Miss L. A. Morgan, Exeter (Library).
E. G. Neal, London (Rongalit white method of staining nerves).
Dr. C. L. Oakley, London (Parasitic copepods).
Dr. C. F. A. Pantin, Cambridge (Neuromuscular action in *Calliactis parasitica*).
J. L. Parkinson, London (Apparatus for osmotic pressure of eggs).
Dr. H. H. Poole, Dublin (Measurement of light).
J. W. S. Pringle, Cambridge (Chemical sense reaction).
J. W. Rees, Aberystwyth (Trematode parasites of Littorina).
C. H. Roberts, Alresford (Oil pollution).
Dr. H. Rosenberg, London (Correlation of electrical responses with histological structure of nerves).
Miss M. L. Rothschild, London (Parasitic Trematodes).
V. Rothschild, Cambridge (Electrical properties of Echinus eggs and fertilisation of Echinus).
A. N. Rowan, London (Correlation of electrical responses with histological structure of nerves).
A. Sandison, Cambridge (Polychaetes).
F. Segrove, Sheffield (Development of Polychaetes).
Dr. B. Sen, Calcutta (Cataphoresis).
Lt.-Col. R. B. Seymour Sewell, Cambridge (Crustacea).
Dr. I. Singh, Cambridge and Rangoon (Plain muscle).
Dr. D. Slome, London (Relation of pituitary to other endocrine organs in fishes).
C. L. Smith, Liverpool (Seawater analysis).
J. E. Smith, Manchester (Nervous system of Asteroids).
Dr. D. Y. Solandt, London and Toronto (Electric excitation of non-medullated nerve. Accommodation process in nerve).
Dr. F. K. Sparrow Junr., Hanover, U.S.A. (Zostera).
Miss F. A. Stanbury, Plymouth (Diatom cultures).
Miss E. M. Stephenson, Exeter (Colour change in prawns).
R. S. Sturdy, Cambridge (Tropisms in Limnea).
Dr. H. Thamdrup, Copenhagen (Fauna of tidal zone).
Prof. T. Tomiyama, Tokyo (Library).
Dr. J. L. Tremblay, Quebec (Plankton).

Miss M. Tribe, London (Eggs).
T. G. Tutin, Kew (Zostera).
Dr. S. L. Vella, Malta (Digestion amongst invertebrates).
H. Vinall, London (Aquarium).
Dr. S. A. Waksman, New Jersey (Diatom cultures and Bacteria).
G. P. Wells, London (Ions and invertebrate muscle. Physiology of Arenicola).
Dr. M. A. Wilson, Plymouth (Marine Algæ).
C. A. Wingfield, London (Colour changes in fishes).
Miss U. Wykes, Oxford (Colour changes in fishes).
Prof. C. M. Yonge, Bristol (Chitin).
J. Z. Young, Oxford (Nervous system of Cephalopods).

The Course in Marine Biology, conducted by Mr. D. P. Wilson and Mr. G. A. Steven, was held as usual during the Easter Vacation, and was attended by forty-one students from Oxford, Cambridge, London, Edinburgh, Sheffield, Newcastle, Liverpool, Manchester, Leeds, Bristol and Exeter.

Also during the Easter Vacation, Dr. A. R. Clapham and Mr. H. Baker conducted a Botanical Class of fourteen students from Oxford University.

During the Summer Vacation, Prof. J. H. Orton conducted a Course of Marine Biology, assisted by Mr. P. H. T. Hartley as Demonstrator. This was attended by twenty students from Oxford, Cambridge, London, Durham, Manchester, Liverpool, Birmingham, Hull, Bristol and Southampton.

During the Easter Vacation, Mr. J. M. Branfoot brought five students from Oundle School; Mr. B. A. Barr, one from Harrow; Mr. H. C. W. Wilson, three from Monkton Combe; Mr. L. V. Turner, one from Rydal School; Mr. A. H. Lewis, three from Wellington College; Mr. R. H. Pott, one from Bradfield College; and Mr. B. W. H. Coulson, two from Dauntsey's School.

At Whitsuntide, a class of seven students was conducted by Dr. E. Idris Jones with Mr. W. H. Leigh-Sharpe from the Chelsea Polytechnic.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment.

The Council desires to place on record its appreciation of the assistance to the work of the Laboratory afforded during the last twelve years by Dr. H. H. Poole, formerly Chief Scientific Officer, and now Registrar of the Royal Dublin Society. During this period Dr. Poole has placed his knowledge of physics and his experience of nautical matters at the disposal of the Staff.

During the last year Dr. Poole has continued his collaboration with Dr. W. R. G. Atkins upon the photo-electric measurement of illumination. Papers embodying the methods of standardizing the cells, the seasonal changes in daylight throughout the year, and other topics mentioned in last year's report have now been published in the Philosophical Transactions of the Royal Society, Series A.

A number of stable photo-cells have been standardized for workers abroad and measurements have thus been made which are strictly comparable with those made in the British Isles. Such information was entirely lacking before and the intensity of tropical illumination was usually much over-estimated. This work has not yet been published. Various types of selenium rectifier cells have been compared and the cell first used has been proved to have remained constant, certainly to within 0·5 per cent, for eighteen months ; during this time it has frequently had long exposures to full sunlight both on shore and on the " Salpa."

Using standardized photo-cells and thermo-piles, determinations have been made of the " luminous efficiency " of mixed daylight, of sunlight and of skylight on the various photo-electric scales. Their agreement with the visual scale has been studied. A special green film filter devised by Dr. L. A. Jones was kindly presented by Dr. C. E. K. Mees, Director of the Kodak Laboratories ; this filter brings the wave-length sensitivity curve of the selenium cell into very good agreement with that of the eye, for light incident normally, but for completely diffused light the extremes are somewhat over-corrected.

Work has been continued on the problem of standardizing combinations of photo-cells and stable filters (so as to divide the solar spectrum into a number of bands), and of measuring the radiation in each in energy units. After several years' consideration the results now obtained can be put forward with a claim to a moderate degree of accuracy. The chief difficulty has lain in the exclusion of the infra-red.

Measurements of submarine illumination have been continued using the modified circuit mentioned in last year's report. The method has been described in the Scientific Proceedings of the Royal Dublin Society. It has worked well and even the near infra-red has been measured down to 11 metres. There are indications that this penetrates rather better than the extreme visible red. The method permits of very rapid work free from error due to atmospheric humidity. The last day's work at sea was carried out in spite of almost continuous rain. Unfortunately a number of otherwise good depth series had to be rejected because the new photometer, far lighter than the old, had been subjected to an error in depth owing to the drift of the ship. The work has however been repeated. Measurements of illumination have also been made for other members of the staff and for visiting workers.

Hydrographic data have continued to be collected in the mouth of the English Channel, and, when observations by cross-channel steamers and other research vessels in the area are published, the general salinity distribution over the area is plotted for each month of the year. An account of the main changes which occur is published at intervals in the Journal.

The investigations on the iron content of sea-water and of marine plankton were continued by Dr. L. H. N. Cooper; 2 : 2′ : 2″–tripyridyl has proved an excellent reagent for the direct determination of iron at high dilutions. Most of the iron in sea-water is in particulate form and theoretical calculations have shown that the concentration of ferric-ion in sea-water is unlikely to exceed 10^{-12} mg. per cubic metre. Diatoms require several times as much iron as phosphorus but the iron requirements of zooplankton are less, much of the ingested iron being excreted. Like silica, the supply of iron appears to be used several times over in the course of one season and may well prove to be a limiting factor in the production of phytoplankton. In view of the considerable demands for iron made by phytoplankton, of the scarcity of ferric and ferrous ions and of the unlikelihood that diatoms can assimilate particles of iron sufficiently coarse to be retained by a membrane filter, it has been suggested that ferrifluoride may provide a suitable source of iron in solution. The results of this work have been published in the Proceedings of the Royal Society, B.

Dissolved organic phosphorus compounds are commonly postulated as intermediates in the breakdown of decaying organic matter to inorganic phosphate, but their importance cannot as yet be properly assessed. The amount present in our waters appears not to be large, but since arsenic is also determined by the analytical methods, it has not yet proved feasible to distinguish between it and "organic phosphorus."

The routine investigation of phosphate-phosphorus (P_2O_5), begun by Dr. Atkins in 1923, has been continued and has borne valuable fruit in connexion with Mr. F. S. Russell's work on plankton distribution. The store of phosphate as shown by the winter maximum, which has to supply the mass of the whole plant and animal community during the ensuing season, has shown marked fluctuations from year to year. A sub-committee of the International Council, of which Dr. Cooper is a member, has been appointed to prepare an account of the methods of chemical analysis used upon sea-water.

Dr. Atkins has developed a method for the quantitative estimation of zinc in fresh and salt waters. The zinc content of sea-water is very low. Miss D. M. Mees has found that 25 parts per million of zinc in sea-water is fatal to small crabs within a few days. Zinc (as from galvanised iron) is readily dissolved by sea water.

Plankton.

The survey of plant and animal plankton per cubic metre of sea, made throughout 1934 at a position 5 miles south-west of the Breakwater by means of a measuring net by Mr. Harvey, Dr. Cooper, Dr. Lebour and Mr. Russell, was continued until after the spring diatom outburst in 1935. The working up of the zoo-plankton material has not yet been fully completed by Mr. Russell.

Arising from this survey, Dr. Cooper has made experiments to investigate what becomes of the phosphorus utilised by diatoms during the early part of the year and not appearing in the summer plankton fauna. Mr. Harvey has made experiments on the possible choice of diatoms by the copepod *Calanus finmarchicus* when fed for a week on one species and then transferred to water containing the same and another species. The feeding rate was obtained for the particular concentrations of diatoms employed.

Mr. Harvey has started an investigation on the effect of varying light and temperature on the growth rate of diatoms. Some quantitative knowledge of this is required to help in interpreting the causes of changes of diatom population in the sea, and is needed before further investigating the effect of varying concentrations of nutrient salts, iron and " auxin " on their growth rate.

In June Mr. F. S. Russell attended the meeting of the International Council for the Exploration of the Sea at Copenhagen, where he had been invited to lecture on " A Review of Some Aspects of Zooplankton Research." This lecture has since been published. Mr. Russell has been appointed to serve on a subcommittee of the Plankton Committee of the International Council and also to serve on the British National Committee of the Pacific Science Association and to act as biological reporter on oceanography.

Mr. Russell has continued his observations on the occurrence of the two species of Sagitta, *S. elegans* and *S. setosa*, off Plymouth. Throughout this year *S. setosa* has still been the predominant species. The real significance of these changes in the Sagitta population has now been brought to light. The examination of a large number of samples taken off the mouth of the English Channel and south of Ireland, kindly supplied by Mr. G. P. Farran, established that *S. setosa* is absent from that area, but *S. elegans* abundant. At the same time there was found to be a certain correlation between the occurrence or absence of *S. elegans* off Plymouth and the direction of flow of water through the Dover Straits as shown by Dr. J. N. Carruthers' drift indicator. It was evident that the two Sagitta species were indicators of different water masses and by examination of the plankton data collected over the past five years it was possible to associate certain other plankton animals as indicators with *S. elegans*. The conclusions and hypothetical deductions arising from this work were published in Vol. XX, No. 2, of the Journal. It was suggested that *S. elegans* would be found to be contained in the water mass previously shown by hydrographers to be in cyclonic circulation off the mouth of the Channel, while *S. setosa* was an indicator of Channel water. To test this suggestion a cruise off the mouth of the Channel was necessary and this became possible in July through the kindness of Col. E. T. Peel, who put his yacht " St. George " at Mr. Russell's disposal. The water mass containing *S. elegans* and its associated species was found to be clearly indicated, and by examination of the plankton content it was possible also to distinguish a body of water entering the Channel past Ushant. The full results of the collection from 28 stations are now ready for publication.

The clearing up of this problem has thrown light on certain other changes off Plymouth. For instance, in recent years there has been a decline in the winter phosphate content of the water. It now appears that the low phosphate values are probably a characteristic of Channel water and as a result the plankton production is limited. The plankton is much richer in *S. elegans* water. It seems possible that the phosphate in Channel water will continue to remain low or decrease until renewed by an invasion of *S. elegans* water such as occurred in 1930 and 1931.

Mr. Russell has also continued his research on the Plymouth medusæ, and has succeeded in rearing the hydroid from *Laodicea undulata*. This has proved to be a Cuspidella species and confirms the earlier work of Metschnikoff and of Delap.

Dr. M. V. Lebour has continued her plankton studies, mainly on the free-swimming gastropod larvæ. A paper is now in the printer's hands bringing together a number of larval forms and eggs hitherto unknown. Accounts of the eggs and larvæ of the Eulimidæ and one on the breeding of *Littorina neritoides* (showing that the latter is not viviparous as hitherto supposed, but has a planktonic egg capsule) have been published in the Association's Journal and a paper on the Echinospira larvæ (Lamellariidæ and Cypraeidæ) in the Proceedings of the Zoological Society. The results of these studies show very plainly that gastropod larvæ are of economic importance in the plankton and occur throughout the year, the species differing in different seasons. In the inside waters the Rissoidæ occupy a prominent position, as well as many others. Further out larger larvæ such as *Nassarius incrassatus*, the Echinospiras, Natica, Simnia and the turrids are the most important. These last all have a well-developed velum often of a complicated form and may remain for a long time in the plankton.

In June a very large number of larval trematodes (*Hemiurus communis*) were taken in a tow-net. These were parasitising the copepod *Acartia clausi*, but many had escaped from their hosts and were moving freely in the water. To see so many at one time is unusual. This worm occurs commonly in the adult state in various gadoids and it is probably eaten by the young fishes in its copepod host during the period when they feed on plankton. Young whiting examined from the plankton measuring up to about three inches in length had all been eating copepods, sometimes in large quantities, and several contained trematodes. A note on this has been published in the Association's Journal.

Attention is still being paid to the larval decapod Crustacea and an hitherto unrecognised larva has been identified as a Spirontocaris different from the one already known. This has led to the study of the adults and it is now found that there are two species in the district where only one, *Spirontocaris cranchi*, was recorded. The second one proves to be a new species, closely related to *S. cranchi* but differing in certain important anatomical structures and in its larvæ. A paper describing the two species and their larvæ, and a comparison with Hippolyte larvæ is now finished and will be published shortly in the Proceedings of the Zoological Society. Another new decapod larva found is a Processa leading to the discovery of two species belonging to that genus previously regarded as one. It is now clearly demonstrable that a large species from the outside waters which is the original *Processa canaliculata* of Leach, and a smaller coastal form, referable to *Processa edulis*, the edible form of the Mediterranean, are present in our fauna, the larvæ of which can be separated easily. A paper describing the two species and their development is ready for publication.

Mr. D. P. Wilson has completed his work on the embryology of the polychaete *Branchiomma vesiculosum*, and a paper has been accepted for publication in the Quarterly Journal of Microscopical Science. He has also prepared, for publication in the Association's Journal, a paper on the development of *Audouinia tentaculata*.

In continuation of his studies on the influence of the substratum on the metamorphosis of annelid worms he has made some experiments with the larvæ of *Notomastus latericeus*, a species which when adult lives in mud or muddy sand. The pelagic life of this larva is relatively short, generally about a week, but varying with the temperature. In these experiments the presence of sand or mud on the bottom of the rearing vessel induced the larvæ to metamorphose a day or two earlier than did the controls left in clean glass dishes. Further work along these lines and with other species would undoubtedly prove of great interest.

Breeding Experiments with Gammarus.

Mrs. Sexton and Miss Clark have been working at the preparation of the report on the study they are making on the origin of recessive characters in *Gammarus chevreuxi* in the wild, and the nature of the variations which occur.

As mentioned in the last report of the Council they were able to show that heterozygosity existed in the wild stock, for red-eyed recessives appeared in the F_1 from the wild. This was the first definite proof obtained, but it was noted at the time that no Red-eye had yet been found in the open, although the possibility of its appearance had been kept in mind for many years past, and dredgings to that end had been made at periodic intervals. They have now to record that success in this also has been obtained for throughout the year marked changes have taken place in the wild stock. In the dredgings of January and February a new mutation appeared affecting the white-pigment cells of the eye—a condition to which the name of " clotted " has been given. In the extreme cases of " clotted " the white pigment runs together into what looks like a clotted mass completely obscuring the ommatidia underneath. The January collection consisted of 81 clotted to 220 normal-eyed; the February one of 35 clotted to 189 normal. An account of this new development has been prepared for publication in the Journal.

The summer dredgings showed very little departure from the normal, but in the autumn dredgings an observation of special interest was made. A large collection was brought in from Chelson Meadow and while it was being examined, a single Red-eyed specimen was found by Mr. Spooner. The remainder of the specimens, numbering 2,039, were Black, and in a dredging taken since then, numbering 800, all were also Black. An interesting point is that this red-eyed specimen was yet another appearance of their Stock II red-eye, which as already noted in 1933 by Mrs. Sexton and Miss Clark (Nature, 131, p. 202), had been spreading through the wild stock.

The material on which their forthcoming report is based was collected in February and March of 1933, when a still greater increase was seen. In twelve stocks changes in the retinal pigment occurred; of these the red-eyed in nine were tested by breeding, and eight were found to be new appearances of the Stock II red; whilst one stock differed from any of the reds previously known. In two stocks, the reds did not survive to maturity, and the remaining one, though still surviving, has never produced enough of the variation to breed from. Changes also took place in the white pigment of the eye, 54 stocks being affected to a greater or less degree. Two only gave the complete genotypic Nowhites; in others non-heritable sporadic cases appeared; in others again, the white pigment was gradually lost, or there was a gradual increase throughout life.

Fish and Fisheries.

Mr. E. Ford followed the progress of the drift-net fishery for herrings at Plymouth during the winter of 1934–35. A total of 91 Lowestoft steamers landed 46,553 cwt. of fish in the two months December, 1934, and January, 1935, representing over 94 per cent of the aggregate weight landed at the port, and leaving only 2,785 cwt. as the total landing by the much reduced fleet of 71 Cornish and local motor drifters. It is doubtful whether the number of West Country boats has ever been fewer, or the yield of their fishing so poor. This falling off in yield of the motor fishery has been in evidence since 1931–32 and seems to be associated with a marked change in character and habit of the visiting shoals. For whereas from 1924–25 to 1930–31, younger fishes from 3 to 6 years of age were always well represented on the grounds and made good fishing for the motor boats in the inshore areas of Bigbury Bay, the shoals from 1931–32 onwards have consisted in the main of older fishes which have remained offshore out of reach of the motor craft, especially in bad weather. These facts are clearly demonstrated by the following figures :—

Season	Percentage No. of Fish at the following ages :—			Average Weight per Landing by :— (cwt.)	
	3 and 4	5 and 6	Over 6	Motors	Steamers
1924–25 to 1929–30	27	51	21	25	32
1930–31	15	57	28	23	33
1931–32	16	36	48	9	18
1932–33	10	25	65	20	34
1933–34	5	30	65	12	30
1934–35	2	23	75	9	28

The comparative absence of fish of the younger year-classes in the Plymouth shoals of the past four seasons implies either that brood-production has failed for a number of years in succession, or that fish of the age of 3, 4 and 5 years no longer come to Plymouth to spawn but go elsewhere. In the former event the drifters are now fishing upon a stock which is yearly growing older and numerically weaker, and must inevitably fall off in yield pending replenishment by new recruits. If, however, younger fish now spawn elsewhere than in the Plymouth area, the success of the future Plymouth fisheries will depend upon the number which at a later period of life make Plymouth their spawning centre. In any case, the new phase of the fishery is an accomplished fact. How long it will last, and what influences brought it about, are problems which await solution. In this connexion the possible correlation with the change in the Sagitta population since 1931 is being kept in mind.

In last year's Report reference was made to an extended programme of herring work, in which Dr. H. Lissner was co-operating, having for its object the study of the relationship between the herrings taken by trawlers and drifters in the waters off the south-western and western coasts, and landed at Fleetwood, Milford, Cornish ports and Plymouth. Representative material was collected in accordance with programme, but as Dr. Lissner left Plymouth to take up an appointment in Turkey, the otoliths collected by him for age estimations have had to be forwarded to him for study as opportunity afforded. Good progress has, however, been made, and the results of the work should soon be available.

In October Mr. Ford attended a meeting at Lowestoft at which herring experts of the countries represented on the International Council for the Exploration of the Sea considered the present state of knowledge concerning the origin and distribution of herring populations in Western Atlantic waters, with a view to the co-ordination of present results and future work. Mr. Ford was given the opportunity of explaining the bearing of his studies of vertebral variation upon the problem of the herring, and was asked to prepare a scheme for testing the practical value of counts of the number of vertebræ in short sections of the vertebral column for population investigations.

Apart from the herring investigations Mr. Ford has continued his studies of vertebral variation in teleost fishes in general, and the preparation of a report. Several additional species have been examined and further specimens of species previously obtained have added to the value of the data on variation from individual to individual.

During the year further attention has been devoted to the problem of growth and migration in Rays and Skates, and a paper embodying the results obtained to date is in course of preparation. In connexion with these experiments Mr. G. A. Steven has been testing out the powers of survival of Rays just under market size after they have been caught in an ordinary commercial trawl. If, immediately after one catch of fish has been brought on board, the trawl be again lowered and the captured fish marked and released while the gear is down, it happens not infrequently that a newly marked fish will go straight to the bottom and be caught again in the trawl. If neither haul exceed about two hours' duration, all except the very smallest fish usually survive this double capture. One individual—a male Thornback 22·5 cm. in width across the wings—was taken three times on the day of marking and has recently been recaptured by the " Salpa " after an absence of eleven months. It was again returned to the sea and is still at liberty.

These results indicate clearly that if trawler skippers could be induced to return all undersized fish to the sea immediately after hauls which are not so long as to kill all but the last-caught fish—much good would be likely to accrue. As the growing fish are not migratory, benefit to the grounds would not be lost through the fish moving elsewhere before reaching marketable size.

Mr. F. S. Russell has continued his observations on the seasonal abundance of the planktonic stages of young fishes. A report on the last five years' work was published in the Journal, Vol. XX, No. 2. In that report, amongst other observations, a decline was shown in the number of young of summer spawning fish. A correlation was shown between the abundance of fish and the quantity of phosphate present in the water in the preceding winter. In the winter of 1934–35 the phosphate values were the lowest yet recorded. The decline in the number of young fish in the summer of 1935 was still continued and in addition the numbers of young of spring spawning fish have dropped considerably. In this respect the correlation between the abundance of young fish and the ultimate food supply available is further strengthened. It now appears from the work on Sagitta that the Channel water in the last few years may have lacked replenishment of phosphate from Atlantic water.

In August Mr. Russell had a further opportunity of spending a week on the North Sea studying Tunny, at the kind invitation of Col. E. T. Peel.

Mr. D. P. Wilson has undertaken a study of certain problems connected with fish flesh as food for human beings, and has made some preliminary studies on the histology of fish muscle, and on the distribution of the histologically stainable fat in various species. This work is in its earliest stages, and at the moment it is inadvisable to make definite statements about the results so far obtained. Mr. Wilson has also made some interesting observations on the habits of three young Anglerfishes (*Lophius piscatorius*) which he has succeeded in keeping in the aquarium. Previously this species has rarely been kept alive in captivity for any length of time, but of the three specimens one survived for over two months, one for three months, and one, which is still alive, for more than six months. During this period this specimen has grown in length from 10½″ to 15″.

Dr. A. Sand has carried out an investigation in collaboration with Dr. J. Gray of Cambridge on the physiology of locomotion in the dogfish, using the cinematographic method. It has been shown that the coordinated muscular rhythm of swimming is determined by a spontaneous rhythmic activity of the spinal cord, which, in the spinal fish, is released from the control of higher centres and gives rise to a persistent undulatory rhythm. The simple reflex behaviour of the spinal dogfish, consisting of a strictly limited number of clearly defined responses, has been described and analysed. These spinal reflexes should provide valuable material for fundamental physiological studies on the spinal cord of Selachians. Dr. Sand has begun an investigation in collaboration with Dr. O. Löwenstein of Birmingham on the function of the semicircular canals in the dogfish. The problem is to analyse the responses of the separate ampullæ of the labyrinth to angular accelerations in different planes. They are using an amplifier and oscillograph kindly lent by Dr. J. Yule Bogue, and a large turntable built for Dr. Löwenstein by the Engineering Department of Birmingham University. The task presents great technical difficulties in view of the small size and inaccessibility of the organs, the high amplification required, and the difficulty of leading off from a moving preparation without microphonic and vibrational disturbances.

Mr. G. M. Spooner has been undertaking a full analysis of the results of experiments conducted last year on the learning of "detours" by young wrasse. The experiments consisted of getting the fish to pass round some glass obstruction on each occasion that food was presented to it. With continual repetition of feeding under identical conditions it was found that usually, sooner or later, the fish developed the habit of moving straight round the obstruction in minimum time, although to start with it had great difficulty in reaching the food at all, and the means by which this was accomplished was largely a chance affair. It was the purpose of the investigation to discover as much as possible about the way in which the efficient response eventually established emerged out of the unorganised responses given in earlier trials. A detailed account was made of every performance; it had to be left for later analysis to show which features were most relevant from the point of view of the acquirement of the learned habit.

The results have been unexpectedly definite in showing that the learning observed was essentially *not* a matter of association of separate response movements, was not, that is, a motor habit; on the contrary, it must have depended on some change in the way the fish sensed its surroundings, some change in the relations which featured in its field of perception. It is interesting to find that the results appear to demand an interpretation of the type suggested by the exponents of the Gestalt theory of sense perception. Attempts have been made in recent years to emphasise that animal learning may be largely a matter of change on the perceptory side of the animal's behaviour activity, but mainly on theoretical grounds, rather than from actual experimental data.

It appears, then, that teleostean fish are capable of the same type of problem learning as exhibited by higher vertebrates and the process by which this learning takes place is essentially comparable.

The information obtained also throws light on other aspects of the wrasse's behaviour capacities. Individual distinctions, for instance, which might otherwise have been unsuspected, came very much into notice. One fish works steadily and persistently; another with a burst of activity that gradually wanes; another is prone to try a number of different movements and does not readily settle down to a uniform performance; and so on. Again, the method proves useful in testing the fish's ability to discriminate visible objects. If the obstruction is invisible, as in the case of plain glass, the fish does not learn to make the detour unless it makes continuous contact with the glass during its sideways movement. If, however, the glass is marked in some way so that its surface has some visible characteristic, the fish comes to move round the glass without making contact at all. By this means it was found that a meshwork of thin scratched lines was readily distinguished.

In August, Mr. G. A. Steven, accompanied by a volunteer assistant, Midshipman G. P. Blake, R.N., carried out a thorough survey of the north coast of Cornwall in order to obtain more precise information concerning the density of its seal population and the species present. He found that the Grey Seal (*Halichoerus grypus*) is the only inhabitant of Cornish waters, and that there are between three and five hundred of them in North Cornwall—i.e. an average of from three to five seals per mile of shoreline. On this coast the seals breed in caves all of which were located and explored.

Advisory work on the preservation of fishing gear and of ropes has been continued by Dr. Atkins. Reports are being prepared upon the results of the examination of preservatives obtained since the last one which was published in 1930. Preservation can be effected more cheaply now, as out of the considerable number of commercial solvents tried one has been found which is both efficient and relatively inexpensive.

Mr. Steven has continued to supervise the experiments on anti-fouling compositions, which are being carried out in co-operation with a firm of paint manufacturers who supply free of charge the compositions with which the " Salpa " is coated.

He has also continued to co-operate in testing the resistance to attack by marine borers of various insulating substances for submarine telegraph cables. Up to the present the experiments indicate that the different types of gutta-percha normally used for insulation purposes are liable to be damaged by boring organisms, especially Gribble (*Limnoria lignorum*).

The resistance of various timbers, treated with Cuprinol as a preservative, is also being tested. It has been found that the grade of Cuprinol known as *Naphtha Green* is a very efficient preventative against attack. One block of Douglas Fir treated with this preservative to the extent of 0·23 gallons per cubic foot has withstood attack over a period of twenty-one months of immersion in gribble-infested water. A piece of the same timber, not treated with preservative, but otherwise subjected to the same conditions, is now badly damaged by gribble. Similar results have been obtained with other timbers treated with this grade of Cuprinol.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated.

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Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1936–37 :—

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Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer.

Guy Wood, Esq., M.B., M.R.C.P., The Charterhouse, London, E.C.1.

Secretary.

E. J. Allen, Esq., C.B.E., D.Sc., F.R.S., The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council:—

G. P. Bidder, Esq., Sc.D.
E. T. Browne, Esq.
The Lord Moyne, P.C. D.S.O.
H. G. Maurice, Esq., C.B. (Ministry of Agriculture and Fisheries).
Major Edward G. Christie-Miller (Prime Warden of the Fishmongers' Company).
Guy Wood, Esq., M.B., M.R.C.P. (Fishmongers' Company).
R. L. Newman, Esq. (Fishmongers' Company).
Prof. E. S. Goodrich, D.Sc., F.R.S. (Oxford University).
J. Gray, Esq., M.C., Sc.D., F.R.S. (Cambridge University).
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S. (British Association).
Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society).
Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society).

List of Annual Subscriptions

Paid during the Year, 1st April, 1935, to 31st March, 1936.

	£	s.	d.
E. J. Allen, Esq., C.B.E., D.SC., F.R.S.	1	1	0
Aquario Vasco da Gama	1	1	0
Prof. J. H. Ashworth, D.SC., F.R.S. (the late)	1	1	0
Miss D. Atkins	1	1	0
W. H. Atkinson, Esq.	1	1	0
Prof. Sir Joseph Barcroft, F.R.S.	1	1	0
G. E. Barnard, Esq.	1	1	0
Miss M. G. Barnes	1	1	0
W. H. Barrett, Esq.	1	1	0
Dr. J. B. Bateman	1	1	0
L. C. Beadle, Esq.	1	1	0
R. L. A. Beauchamp, Esq.	1	1	0
G. R. de Beer, Esq.	1	1	0
J. Bělehrádek, Esq., M.D.	1	1	0
D. M. Bickmore, Esq. (1936 and 1937)	2	2	0
Birkbeck College	1	1	0
W. Birtwistle, Esq.	1	1	0
Dr. H. Blaschko (1935 and 1936)	2	2	0
H. H. Bloomer, Esq.	1	1	0
H. Moss Blundell, Esq., C.B.E.	1	1	0
Mrs. H. Moss Blundell	1	1	0
Dr. B. G. Bogorov (1933 and 1936)	2	2	0
Capt. R. J. B. Bolitho	1	1	0
J. R. Bolton, Esq.	1	1	0
Dr. J. Borowik	1	1	0
L. A. Borradaile, Esq., SC.D.	1	1	0
S. J. A. Bosanquet, Esq. (1935 and 1936)	2	2	0
Prof. C. L. Boulenger	1	1	0
Col. Sir Henry Bowles, Bart.	1	1	0
A. Bowman, Esq., D.SC.	1	1	0
Prof. A. E. Boycott, F.R.S.	1	1	0
E. Boyland, Esq.	1	1	0
Miss B. L. Boyle	1	1	0
J. M. Branfoot, Esq. (1934 and 1935)	2	2	0
Carried forward	40	19	0

	£	s.	d.
Brought forward	40	19	0
Brighton Public Library	1	1	0
L. R. Brightwell, Esq.	1	1	0
Bristol University	1	1	0
Miss E. M. Brown	1	1	0
R. Brown, Esq.	1	1	0
Dr. H. O. Bull	1	1	0
R. H. Burne, Esq., F.R.S.	1	1	0
M. Burton, Esq.	1	1	0
R. R. Butler, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Prof. H. Graham Cannon, SC.D., F.R.S.	1	1	0
J. N. Carruthers, Esq., D.SC.	1	1	0
Dr. G. S. Carter, (1933, 1934, 1935 and 1936)	4	1	0
Paymaster-Captain R. Charles, R.N. (retd.)	1	1	0
Charterhouse School	1	1	0
R. G. Church, Esq.	1	1	0
R. S. Clark, Esq., D.SC.	1	1	0
Coastguard and Fisheries Service, Alexandria	1	1	0
Prof. F. J. Cole, D.SC., F.R.S.	1	1	0
H. A. Cole, Esq.	1	1	0
J. S. Colman, Esq.	1	1	0
Sub-Lieut. R. Connell, R.N.	1	1	0
J. Omer Cooper, Esq. (1932, 1933, 1934, 1935 and 1936)	5	0	0
Col. R. Stapleton-Cotton	1	1	0
G. I. Crawford, Esq.	1	1	0
L. R. Crawshay, Esq.	1	1	0
Miss D. R. Crofts	1	1	0
Sir Henry H. Dale, C.B.E., M.D., F.R.S. (1933, 1934, 1935 and 1936)	4	4	0
Dr. H. H. Darby (1932, 1933 and 1934)	3	3	0
F. M. Davis, Esq. (1934 and 1935)	2	2	0
B. Dawes, Esq., D.SC.	1	1	0
Department of Fisheries, Bangkok	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
Miss N. B. Eales, D.SC.	1	1	0
Prof. L. E. S. Eastham	1	1	0
P. Eggleton, Esq., D.SC.	1	1	0
The Rt. Hon. Walter E. Elliot, M.C., M.P., F.R.S.	1	1	0
C. E. D. Enoch, Esq. (1934 and 1935)	2	2	0
G. P. Farran, Esq.	1	1	0
Carried forward	96	4	0

	£	s.	d.
Brought forward	96	4	0
Miss R. Fellowes	1	1	0
Prof. R. A. Fisher, SC.D., F.R.S.	1	1	0
Fisheries Survey Committee, Capetown	1	1	0
Miss K. M. G. Fleming	1	1	0
E. Ford, Esq.	1	1	0
E. B. Ford, Esq. (1935 and 1936)	2	2	0
Dr. G. Herbert Fowler	1	1	0
C. L. Fox, Esq.	1	1	0
Dr. E. L. Fox	1	1	0
Prof. H. Munro Fox	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
F. C. Fraser, Esq.	1	1	0
Prof. F. E. Fritsch, F.R.S.	1	1	0
Prof. J. Stanley Gardiner, F.R.S. (1935 and 1936)	2	2	0
A. Gardner, Esq.	1	1	0
Ghardaqa Marine Laboratory (1935 and 1936)	2	2	0
H. C. Gilson, Esq. (1935 and 1936)	2	2	0
Prof. E. S. Goodrich, D.SC., F.R.S.	1	1	0
Alastair Graham, Esq.	1	1	0
Michael Graham, Esq.	1	1	0
Ronald Grant, Esq.	1	1	0
Dr. A. M. H. Gray	1	1	0
J. Gray, Esq., M.C., SC.D., F.R.S.	1	1	0
H. P. Hacker, Esq., M.D., D.SC.	1	1	0
Prof. A. C. Hardy	1	1	0
Prof. C. R. Harington, F.R.S.	1	1	0
J. E. Harris, Esq.	1	1	0
T. J. Hart, Esq.	1	1	0
P. H. T. Hartley, Esq.	1	1	0
Prof. L. A. Harvey	1	1	0
Dr. G. T. D. Henderson	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq.	1	1	0
Prof. Sydney J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
F. R. Horne, Esq.	1	1	0
H. D. Howell, Esq.	1	1	0
N. H. Howes, Esq. (1935 and 1936)	2	2	0
Carried forward	142	8	0

	£	s.	d.
Brought forward	142	8	0
P. Hoyte, Esq.	1	1	0
Hull University College	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. J. S. Huxley	1	1	0
Miss P. M. Jenkin	1	1	0
Miss M. Jepps	1	1	0
D. D. John, Esq.	1	1	0
J. J. Judge, Esq.	1	1	0
Stanley Kemp, Esq., Sc.D., F.R.S.	1	1	0
Mrs. A. Redman King	1	1	0
P. Kirtisinghe, Esq.	1	1	0
Dr. J. A. Kitching	1	1	0
Dr. G. Lapage	1	1	0
Prof. R. D. Laurie	1	1	0
D. W. Le Mare (1936 and 1937)	2	2	0
A. G. Lowndes, Esq.	1	1	0
C. E. Lucas, Esq. (1935 and 1936)	2	2	0
Adrian Lumley, Esq.	1	1	0
Prof. E. W. MacBride, D.Sc., F.R.S. (1935 and 1936)	2	2	0
Lieut.-Col. W. Mackenzie, O.B.E. (1936, 1937 and 1938)	3	3	0
Prof. D. L. Mackinnon, D.Sc.	1	1	0
G. I. Mann, Esq.	1	1	0
B. J. Marples, Esq.	1	1	0
Sir John D. Marsden, Bart., J.P.	1	1	0
D. J. Matthews, Esq.	1	1	0
H. G. Maurice, Esq., C.B. (1931, 1932, 1933, 1934, 1935 and 1936)	6	6	0
Capt. W. N. McClean	1	1	0
C. R. McKenzie, Esq.	1	1	0
Milford Haven Trawler Owners' Association Limited	1	1	0
W. S. Millard, Esq.	1	1	0
Dr. G. A. Millikan	1	1	0
Norman Millot, Esq.	1	1	0
Sir P. Chalmers Mitchell, Kt., C.B.E., D.Sc., F.R.S.	1	1	0
Mrs. E. M. Morehouse	1	1	0
C. C. Morley, Esq.	1	1	0
Mount Desert Island Biological Laboratory	1	1	0
Dr. J. Mukerji	1	1	0
National Museum of Wales, Cardiff	1	1	0
Morley H. Neale, Esq.	1	1	0
Carried forward	193	17	0

	£	s.	d.
Brought forward	193	17	0
Messrs. Neale and West, Limited	1	1	0
Dr. A. G. Nicholls	1	1	0
J. A. Nicholson, Esq.	1	1	0
J. R. Norman, Esq.	1	1	0
Dr. C. L. Oakley	1	1	0
Office Scientifique et Technique des Pêches Maritimes, Port de l'Orient Keroman	1	1	0
Office Scientifique et Technique des Pêches Maritimes, La Rochelle (1935 and 1936)	2	2	0
Chas. Oldham, Esq.	1	1	0
G. W. Olive, Esq.	1	1	0
Prof. J. H. Orton, D.SC.	1	1	0
R. Palmer, Esq. (1933, 1934 and 1935)	3	3	0
The Hon. John H. Parker	1	1	0
C. W. Parsons, Esq.	1	1	0
Messrs. Pawlyn Bros.	1	1	0
T. A. Pawlyn, Esq.	1	1	0
Messrs. Peacock and Buchan, Limited	1	1	0
Pease Laboratories Incorporated	1	1	0
Col. E. T. Peel, D.S.O., M.C.	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Prof. E. Percival	1	1	0
L. E. R. Picken, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Educational Authority	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
Portsmouth Municipal College	1	1	0
Dr. H. E. Quick, F.R.C.S.	1	1	0
Dr. A. Ramalho	1	1	0
W. J. Rees, Esq.	1	1	0
H. C. Regnart, Esq.	1	1	0
D. M. Reid, Esq.	1	1	0
Prof. L. P. W. Renouf	1	1	0
E. A. Robbins, Esq. (1935 and 1936)	2	2	0
Victor Rothschild, Esq.	1	1	0
C. H. Rudge, Esq. (1936 and 1937)	2	2	0
E. S. Russell, Esq., D.SC.	1	1	0
F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
Carried forward	237	19	0

	£	s.	d.
Brought forward	237	19	0
Capt. the Hon. Lionel St. Aubyn, M.V.O.	1	1	0
The Rt. Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
Dr. A. Sand (1935 and 1936)	2	2	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
Dr. F. F. Schacht	1	1	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
B. Sen, Esq.	1	1	0
Miss Lilian Sheldon	1	1	0
Prof. W. Rae Sherriffs, D.SC.	1	1	0
H. P. Sherwood, Esq.	1	1	0
B. Webster Smith, Esq. (part 1934 and 1935)	1	11	6
F. G. W. Smith, Esq.	1	1	0
J. E. Smith, Esq.	1	1	0
V. D. Van Someren, Esq.	1	1	0
G. M. Spooner, Esq.	1	1	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	3
Prof. T. A. Stephenson, D.SC. (1934 and 1935)	1	19	6
Mrs. G. A. Steven	1	1	0
C. Stewart-Evison, Esq.	1	1	0
Mrs. R. S. Sturdy	1	1	0
E. J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
Harold Thompson, Esq., D.SC.	1	1	0
Sir Herbert F. Thompson, Bart.	1	1	0
Torquay Natural History Society	1	1	0
Miss E. M. Tregoning	1	1	0
Phillip Ullyott, Esq.	1	1	0
J. L. Tremblay, Esq., D.SC.	1	1	0
Prof. S. L. Vella	1	1	0
R. C. Vernon, Esq. (1935 and 1936)	2	2	0
H. M. Vickers, Esq. (1935 and 1936)	2	2	0
Dr. A. Walton	1	1	0
Carried forward	283	10	0

	£	s.	d.
Brought forward	283	10	0
Sir Nicholas E. Waterhouse, K.B.E.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
G. Weaver, Esq.	1	1	0
Mrs. F. J. Weldon	1	1	0
Miss K. M. White	1	1	0
P. H. F. White, Esq. (1935 and 1936)	2	2	0
D. P. Wilson, Esq.	1	1	0
Mrs. D. P. Wilson, PH.D.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
Total	£298	4	3

List of Donations to the General Fund

For the Year, 1st April, 1935, to 31st March, 1936.

	£	s.	d.
D. M. Bickmore, Esq.	1	0	0
British International Pictures, Ltd.	5	0	0
Messrs. Ivor, Nicholson and Watson, Ltd.	1	1	0
Dr. C. L. Oakley	1	1	0
Total	£8	2	0

List of Composition Fees

Paid during the Year, 1st April, 1935, to 31st March, 1936.

	£	s.	d.
Dr. C. Amirthalingam	15	15	0
J. H. Fraser, Esq.	15	15	0
Total	£31	10	0

THE MARINE BIOLOGICAL ASSOCIATION

INCOME AND EXPENDITURE ACCOUNT

	£	s.	d.	£	s.	d.
To SALARIES, including Institution's Contributions to Superannuation				7,560	11	7
,, LABORATORY WAGES, including National Insurance and Institution's Contributions to Superannuation ..				2,278	14	9
,, DEPRECIATION OF LIBRARY				500	1	6
,, SCIENTIFIC PUBLICATIONS, *Less* SALES				452	18	10
,, UPKEEP OF LABORATORIES AND TANK ROOMS:						
Buildings and Machinery	269	13	8			
Electricity, Gas, Coal, Oil and Water	367	4	10			
Chemicals and Apparatus	330	16	11			
Rates, Taxes and Insurance	105	6	7			
Travelling Expenses	88	19	1			
Stationery, Postages, Telephone, Carriage and Sundries	362	18	5			
Specimens	117	0	6			
				1,642	0	0
,, MAINTENANCE AND HIRE OF BOATS:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1,683	14	3			
Coal, Water, Oil, Petrol, etc.	278	16	8			
Maintenance and Repairs with Nets, Gear and Apparatus	492	15	2			
Purchase of Material for Nets for Sale, excluding Labour	190	7	6			
Boat Hire and Collecting Expenses	25	18	11			
Insurance	276	7	0			
				2,947	19	6
,, TRANSFER TO DEPRECIATION RESERVE ACCOUNT ..				300	18	6
,, TRANSFER TO CORNWALL SEAL INVESTIGATIONS ..				1	6	8
,, BALANCE, BEING SURPLUS FOR THE YEAR				268	16	9
				£15,953	8	1

OF THE UNITED KINGDOM.

YEAR ENDED 31st MARCH, 1936.

	£	s.	d.	£	s.	d.
By Grants :						
Ministry of Agriculture and Fisheries Grant from Development Fund	12,085	4	6			
Fishmongers' Company	600	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0			
Cornwall Sea Fisheries Committee	20	0	0			
				12,835	4	6
,, Subscriptions Received During the Year ..	298	4	3			
Less : Proportion received in advance	111	11	3			
				186	13	0
,, Donations				8	2	0
,, Sales :						
Specimens	1,309	9	0			
Fish (*less* expenses)	65	5	9			
Nets, Gear and Hydrographical Apparatus	340	9	8			
				1,715	4	5
,, Table Rents (including University of Cambridge £105 ; Oxford £52 10s. 0d. ; London £52 10s. 0d. ; Bristol £25 ; Birmingham £15 15s. 0d. ; Manchester £10 10s. 0d. ; Leeds £10 10s. 0d. ; Imperial College £10 ; Sheffield £5 5s. 0d. ; Trustees of Ray Lankester Fund £20)..				540	19	4
,, Tank Room Receipts				586	4	3
,, Interest on Investments, Less Tax :						
General Fund	20	18	3			
Depreciation Fund	28	17	4			
Composition Fee Fund	2	5	1			
				52	0	8
,, Interest on Bank Deposit Account (*less* Bank Charges)				1	11	3
,, Sale of Dr. M. V. Lebour's Book	4	7	6			
,, Sale of "Marine Fauna of Plymouth"	8	0	0			
				12	7	6
,, Income Tax Recoverable				15	1	2
				£15,953	8	1

BALANCE SHEET

	£	s.	d.	£	s.	d.
Sundry Creditors :						
On Open Account				127	8	6
Proportion of Subscriptions Received in Advance..				111	11	3
Jewish Scholarship Fund :						
As at 31st March, 1935	59	19	2			
Add : Third Instalment received	100	0	0			
	159	19	2			
Less : Expenditure..	92	6	10	67	12	4
E. T. Browne Special Donation Fund :						
As at 31st March, 1935	13	3	5			
Less : Expenditure..	13	3	5	–	–	–
Aquarium Guide Printing Fund :						
As at 31st March, 1935	31	5	0			
Donations received	10	0	0			
Sale of Aquarium Guides	14	10	0			
	55	15	0			
Less : Expenditure..	48	14	0	7	1	0
Dr. H. B. Moore Special Grant Fund :						
Grant received	300	0	0			
Less : Expenditure..	300	0	0	–	–	–
T. G. Tutin Special Grant Fund :						
Grant received	187	10	0			
Less : Expenditure..	177	1	8	10	8	4
E. T. Browne Special Grant Fund :						
Grant received	400	0	0			
Less : Expenditure..	69	15	0	330	5	0
Cornwall Seal Investigations :						
Grant received	25	0	0			
Transfer from Income and Expenditure Account ..	1	6	8			
	26	6	8			
Less : Expenditure..	26	6	8	–	–	–
Reserve for Depreciation of Boats and Machinery :						
As at 31st March, 1935	1,158	17	11			
Add : Transfer from Income and Expenditure Account	300	18	6	1,459	16	5
Composition Fee Fund :						
Transfer from General Surplus as at 31st March, 1935 ..	94	10	0			
Add : Received during the year	31	10	0	126	0	0
Surplus :						
As at 31st March, 1935	6,331	9	8			
Less : Transfer of Composition Fees	94	10	0			
	6,236	19	8			
Add : Surplus for the year as per Income and Expenditure Account	268	16	9	6,505	16	5
				£8,745	19	3

(Signed) C. M. Yonge } *Members of Council.*
G. P. Wells

To the Members of the Marine Biological Association of the United Kingdom :

We report that we have examined the above Balance Sheet with the books of the
Capital expenditure on erection of Buildings on Land held on Lease from the War
Sheet is properly drawn up so as to exhibit a true and correct view of the state of the
given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
Plymouth. 20*th April,* 1936.

31st MARCH, 1936

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, as per Valuation as estimated by the Director at 31st March, 1931						
S.S. *Salpa*	2,000	0	0			
Motor Boat	150	0	0			
Nets, Gear and General Equipment	27	0	0			
				2,177	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS:						
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at Cost						
As at 31st March, 1935	673	13	11			
Additions during the year (Net)	157	13	6			
				831	7	5
LIBRARY:						
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at Cost less Depreciation						
As at 31st March, 1935	2,196	4	10			
Additions during the year	560	18	0			
	2,757	2	10			
Less: Depreciation	500	1	6			
				2,257	1	4
STOCK OF SPECIMENS, CHEMICALS AND JOURNALS						
As estimated by the Director				375	0	0
SUNDRY DEBTORS:						
Sale of Specimens and Journals	220	13	10			
Grant	30	0	0			
				250	13	10
INCOME TAX RECOVERABLE				5	18	7
PREPAYMENTS				103	4	3
GENERAL FUND INVESTMENTS at Market Value as at 31st March, 1931:						
£410 14s. 8d. New Zealand 4% 1943/63	344	15	0			
£352 2s. 3d. Local Loans 3%	232	7	10			
(Market Value at date £770 3s. 7d.)				577	2	10
DEPRECIATION FUND INVESTMENTS at Cost:						
£590 6s. 0d. Local Loans 3%	506	10	9			
£916 3s. 4d. Conversion Loan 3%	931	5	8			
(Market Value at date £1,530 2s. 9d.)				1,437	16	5
COMPOSITION FUND INVESTMENTS at Cost:						
£18 8s. 6d. Local Loans 3%	15	15	0			
£108 6s. 5d. Conversion Loan 3%	110	5	0			
(Market Value at date £131 9s. 5d.)				126	0	0
CASH AT BANK AND IN HAND:						
Coutts & Co.—Current Account	14	1	8			
,, Deposit Account	335	15	0			
Lloyds Bank Limited	226	13	1			
Cash in Hand	28	4	10			
				604	14	7
				£8,745	19	3

Association and have obtained all the information and explanations we have required. Department is excluded. Subject to this remark we are of opinion that the Balance Association's affairs, according to the best of our information and the explanations

(Signed) PRICE, WATERHOUSE & Co.

SEP 1954
LIBRARY
POFI
FISH & WILDLIFE
SERVICE

The Habits of the Angler-fish, *Lophius piscatorius* L., in the Plymouth Aquarium.

By
Douglas P. Wilson, M.Sc.,
Naturalist at the Plymouth Laboratory.

With Plate I and 2 Figures in the Text.

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INTRODUCTION.

THE Angler-fish (*Lophius piscatorius* L.), also known as the Fishing-frog, Monk-fish, Sea-devil, etc., is notoriously difficult to keep in captivity. It has rarely survived in an aquarium for any length of time and published accounts of observations made from life are somewhat conflicting. Much that has been written about the habits of the species has been based on deduction from the structural features of dead specimens. It seems therefore worth while putting on record the details of some recent observations made at Plymouth, where a number of angler-fishes have been kept alive and in health for periods varying from a few weeks to nearly a year.

Although living angler-fishes are regularly brought ashore by the S.S. *Salpa* very few survive for more than a few hours. It is probable that the soft and flabby nature of the body, particularly of the abdominal wall, exposes the fish to severe internal injuries in the trawl. All survivors have been small and had apparently in some way escaped the usual bruising that takes place when the cod-end is hauled. It is noteworthy that one brought up in unusually good condition was taken in a small Agassiz trawl, an instrument which is much less severe on its captives.

The colour of a healthy angler-fish generally distinguishes it at once from those that are dead or dying. The latter exhibit a fine speckling of pigment that from a little distance imparts an almost uniform chocolate brown appearance to the greater part of the head and back. In a healthy specimen the colour is usually paler and yellower, being often coarsely mottled with light and dark patches, especially when it has presumably come off a gravelly bottom.

With the exception of the first specimen (later referred to as Angler-fish No. 1) all have been kept in a glass-fronted slate table-tank, five feet long, two feet four inches wide, and with a water depth of nearly fifteen inches. The greater part of the bottom was thickly strewn with a gravelly sand containing much fragmented shell (see Plate I): at one end there were a few large rocks. A few small starfishes, Aphrodite, Scaphander Holothuria, and some small fishes shared the tank.

In nearly every instance hand feeding was necessary for the first few weeks, because living fishes of species attractive to angler-fishes were not at the time available. Dead wrasses (generally *Ctenolabrus rupestris*, sometimes *Labrus bergylta*), gobies (*Gobius minutus* and *G. paganellus*), and an occasional gadoid were given. As remarked later some individuals took more readily to this treatment than did others. The fish was always inserted into the angler's mouth head first. If the jaws gripped it, it would almost invariably be swallowed, but very frequently the mouth would be opened as wide as possible and by a convulsive movement the food " coughed " out. Repeated insertions might be necessary before the angler-fish would bite. One or two angler-fishes that were at first difficult to feed seemed to learn through experience and later on gave, on the whole, less trouble.

In order to make observations on the use of the lure living fish were from time to time placed in the tank. If newly caught from the sea, however, they would be too bruised and frightened to react to the angler's lure. Fish netted from a tank where they had lived for some time were better, but even so were generally too scared to behave naturally. Removing the angler-fishes themselves to a tank containing small fishes, which had been living there long enough to be fully accustomed to their surroundings, gave greatly improved results. This tank was twice the length of the angler's own and was strewn with sand; it housed starfishes of several kinds and some Corystes crabs. The angler-fishes were never seriously disturbed by their transference (in a large bowl of water) and would usually at once settle themselves in a sandy hollow and begin to fish.

I should specially like to thank Capt. V. Lord and the crew of the S.S. *Salpa* for the care they have taken with the angler-fishes they have caught alive. Mr. G. M. Spooner has from time to time attended them, and kept notes for me when I have been away, and to him I am also grateful.

HISTORICAL.

The literature relating to angler-fishes and their habits is extensive. From Aristotle onwards the curiosity of naturalists has been aroused, but few writers appear to have watched the fish alive, either in its natural environment or in the confines of an aquarium tank, and many stories of its habits are based largely or solely on imagination. I propose to mention here chiefly those more recent authors who have recorded observations on the living animal.

One cannot, however, ignore Aristotle. His remarks show that he must have spent much time watching the creature through the surface of the sea. He saw angler-fishes stirring up the sand and mud when settling themselves on the bottom; he saw the dorsal fin-rays used as baits, and the capture of little fishes. He records the unusual thinness of angler-fishes caught after the loss of the tips of their fishing rods. All that later writers can do is to amplify his remarks by filling in the details.

In more modern times a few naturalists have made some first-hand observations. In 1874 Saville Kent kept an angler --apparently for a few days only—in the old Manchester Aquarium. He compared it to a rock, the irregular bordering tags of skin resembling Grantia, ascidians, etc., organisms such as hang down from rocky ledges. The dorsal spines he likened to young Laminaria fronds, and the eyes to acorn-barnacles. He apparently did not see his specimen feed, but supposed that fishes misled by this mimicry would approach near enough to be snapped up: he seems to have doubted stories of angling activities.

Guitel (1891) kept a Lophius, sixty centimetres long, for two months in the laboratory aquarium at Arago. He never saw the lure in use; it was always folded back out of the way. His fish captured a bass half its own length and two large Sargus fishes when they happened to swim too close above the mouth.

Bigelow and Welsh (1925) record some observations by W. F. Clapp, who frequently watched the feeding habits of this fish at low-tide in Duxbury Bay, Mass. It is described as lying motionless among the eelgrass with the " bait on the tip of the first dorsal ray swaying to and fro over the mouth, either with the current or by some voluntary motion so slight as to be invisible." It was observed to take tomcod (*Microgadus tomcod* Walbaum) which were caught when they swam too near to the bait. The species of angler-fish here mentioned is given as *Lophius piscatorius* Linnæus, but Berrill (1929) has more recently brought forward strong evidence to support an earlier conclusion that the American angler-fish is distinct from the European and should be named *L. americanus* Valenciennes.

Dahlgren (1928), in a popular account of the habits and life-history of the angler, mentions that he has watched numbers of this fish tethered alive in the sea close to the Mount Desert Island Laboratory. He describes how they were there attacked by starfishes and sea-urchins, which ate away patches of their skin. Dahlgren did not see his anglers feed and he definitely states (p. 22) that no one has seen a Lophius feed while confined in an aquarium. " He makes a poor aquarium subject since he refuses all food in captivity, and hence does not live long." Dahlgren points out the paucity of original observations on the use of the lure for fishing since Aristotle made the first statement about it.

The most important recent observations are those of Chadwick (1929), who gives a short, but very accurate account of the feeding habits of angler-fishes in the Port Erin aquarium. He repeatedly saw them use the lure to attract coal-fishes (*Gadus virens*), which they seized and swallowed head first.

Finally one gathers from a popular article (Weller, 1934) that living angler-fishes are occasionally exhibited in the Brighton Aquarium, and that they are there fed on flat-fishes attracted by the lure. The species has also been exhibited in the Zoological Society's aquarium at Regent's Park (Boulenger, 1932) but survived for only a few days, evidently not feeding.

INDIVIDUAL HISTORIES.

During the past two years about ten angler-fishes have lived, apparently in good health, in the Plymouth aquarium. Of these only five have survived longer than a few weeks: some particulars of their histories are given below.

Angler-fish No. 1.

Caught: first week in January, 1935.
Died: 8th April, 1935.
Length when caught: 6 inches.
Length at death: 7¼ inches.

During the first part of its captivity it lived in a bowl strewn with shelly gravel and placed under circulation from a sea-water jet. Later it was exhibited in a small tank in the public part of the aquarium. For the first ten days no food was taken although living *Gobius minutus* and small flat-fishes were supplied. Hand feeding was then resorted to, the mouth being held open while a fish was inserted. While at first it was difficult to induce the angler to accept food, this later became easier, and it was no longer necessary to force open the mouth. This angler was never known to catch prey for itself. A photograph of it, taken within a fortnight of capture, is reproduced elsewhere (Wilson, 1935, Fig. 80).

Angler-fish No. 2.

Caught: 18th April, 1935. Died: 17th March, 1936.
Length when caught: 10½ inches.
Length on 7th November, 1935: 15 inches.
Length on 10th January, 1936: 17½ inches.
Length at death: 18¼ inches.

This specimen, like all subsequent ones, was placed in the tank already described (p. 478) as soon as it was brought in. For about the first month it was every two days or so placed in a bowl and removed from the tank for convenient feeding by hand. Later it was allowed to catch living fish for itself. It was often seen to fish with the lure, except during the last few months when it always waited until prey chanced to wander, or was driven, within reach. This angler, like the first, was very docile and easy to handle, never snapping at the fingers when fed by hand. It finally succumbed to disease.

Angler-fish No. 3.

Caught: 3rd September, 1935.
Died: 16th November, 1935.
Length when caught: 8 inches.
Length at death: 10½ inches.

At first fed on dead fish given by hand or forceps, it later refused such proffered food and apparently subsisted on living *Gobius minutus*, which were put into the tank and which it must have caught for itself. It was often seen using its fishing lure and once or twice was observed to catch a goby that came too near. A post-mortem revealed two half-digested *Gobius minutus* in the stomach and unidentifiable remains in the intestine. Cause of death unknown.

This specimen was rather vicious and would snap fiercely at food presented with the forceps; it was not safe to give food with the fingers.

Angler-fish No. 4.

Caught: 17th December, 1935.
Died: 25th March, 1936.
Length on capture: 11¼ inches.
Length at death: 13 inches.

Unlike the last this fish never snapped when hand-fed and was quite docile. It was very easy to feed, generally accepting dead fish readily when living were not available and rarely "coughing" them out again. It gave very fine displays of its angling abilities, and on it, more than on any other single specimen, my account of this habit is based. It eventually died from the disease that killed No. 2 as well as one other angler-fish not specially mentioned in this paper. This disease was evidently highly infectious; the skin and underlying tissues of the head swelling rapidly, becoming soft and gelatinous, and finally peeling away to the bone, death ensuing within a few days.

Angler-fish No. 5.

Caught: 29th January, 1936.
Died: 24th May, 1936.
Length on capture: 10½ inches.
Length at death: 12½ inches.

This was first fed by hand on dead fish which were occasionally accepted but more often refused, being "coughed" out repeatedly. There is little doubt that it caught and ate the *Gobius minutus* living in the same tank. It was often seen with the rod held horizontally forwards above the closed mouth as if in readiness to fish, but was never actually observed to catch anything. It died by jumping out of the tank during the night, having been saved from the disease that killed Nos. 2 and 4 by being isolated from them. A post-mortem revealed remains of food, including an otolith in the intestines.

The remaining angler-fishes need not be specially mentioned. They were very useful in checking observations made on these five, and added some details to them. One, caught early in July, 1936, and suddenly dying for no apparent cause about five weeks later, is shown in Plate I. This photograph was taken when it appeared to be in perfect health eleven days before death. At that time it was expected to live for at least several months.

Angler-fishes show strong individual characteristics, especially as regards their habits and reactions. While some are sharp tempered and snap readily at any object, such as a ruler pushed towards them, others are very quiet and docile. Some readily swallow dead fishes placed in their mouths, others do not. Some angle with the lure much more frequently and readily than do others. One or two specimens have made little or no use of the lure, at least while being watched. Certain individuals seemed much more inclined than most to sit about on the rocks at one side of their tank. In short, no two anglers behaved exactly alike.

Growth.

In Figure 1 are shown graphically the length increases of the five angler-fishes whose histories have just been given. Except for No. 2 only the lengths at capture and at death are plotted. Frequent measurements were not taken as they were scarcely practicable. It is extremely difficult to measure a living angler at all accurately, especially at the bottom of a tank where the ruler has to be balanced horizontally on the rounded upper surface of the angler's head. The amount of closure of the mouth may make a slight difference. The limits of error are probably an eighth of an inch or a little more either way. For this reason too much reliance should not be placed on the exact slopes of the growth lines as shown. Nevertheless the relatively rapid growth of No. 3 as compared with the others might be due to the fact that it took place when the tank temperature was higher than at the times when Nos. 1, 4, and 5 were kept. On the other hand the rapid growth of No. 2 between 7th November, 1935, and 10th January, 1936, scarcely justifies such a conclusion.

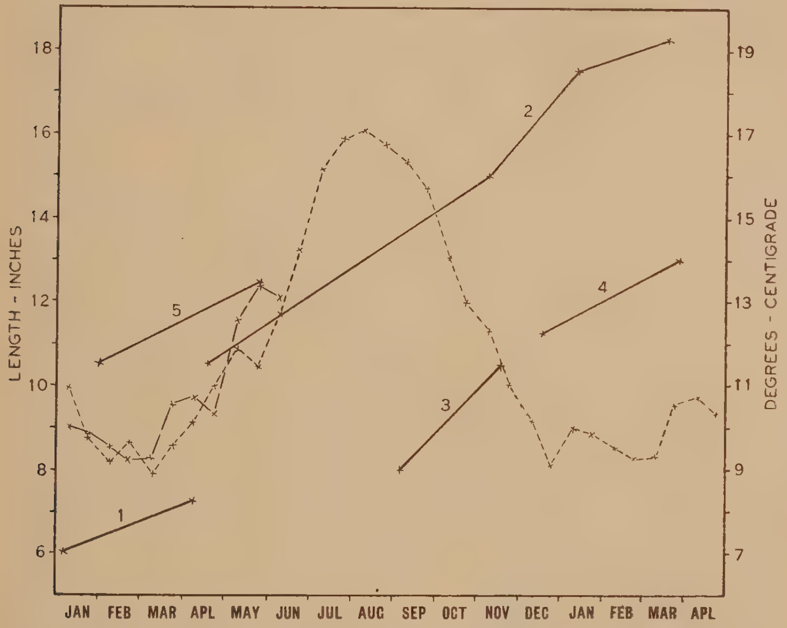

Fig. 1.—Growth of the five angler-fishes mentioned in the text shown by continuous lines. Broken lines represent tank temperatures from January, 1935, to June, 1936. Temperatures from January, 1936, to June, 1935, are plotted on the left and the points joined by longer broken lines. Each plotted point is an average fortnightly temperature calculated from daily readings taken by Mr. A. J. Smith.

Angler-fish No. 2 increased in length by $7\frac{3}{4}$ inches in almost exactly eleven months, giving an annual increment of about $8\frac{1}{2}$ inches per year. The other four fishes lived for much shorter periods than this, but all appear to have been growing at approximately similar rates.

In assessing the value of these growth data for young angler-fishes kept under aquarium conditions it should be remembered that all were carefully fed and probably on the whole got as much food as they wanted. The temperature curve given is based on regular readings taken in an aquarium tank in another part of the building. Although all tanks exhibit slight individual temperature variations they are on the same circulatory system, and it is known that their average temperatures do not materially differ, but all follow the same general curve. Thus this curve should represent quite closely the conditions that occurred in the angler-fish tank itself.

Fulton (1903) has attempted to assess the growth rate of Lophius in the northern North Sea. By measuring specimens trawled in all months of the year he has estimated, admittedly on somewhat scanty data, that the mean annual increment in length is a little over 6 inches, this for angler-fishes ranging from about 6 to 18 inches long. He considered that anglers of a mean length of $6\frac{3}{4}$ inches would be approximately six months old; a year later the mean length reaches about $12\frac{1}{2}$ inches, and at two years six months 18–$18\frac{1}{2}$ inches.

It will be noted that Fulton's fishes were of the same size range as mine. Although it is always dangerous to compare growth in an aquarium with growth in the sea it is not without interest that his estimate of annual growth is of the same order as that which actually took place in captivity. If one could assume that both his anglers and mine obtained as much food as they felt naturally urged to eat, the difference between his smaller estimate and my records might conceivably be regarded as due to a difference in temperature. Bottom water in the northern North Sea is considerably colder throughout the year than that circulating in the Plymouth aquarium.

MOVEMENTS AND CAMOUFLAGE.

As has been often remarked by other writers angler-fishes are very poor swimmers. They can get along moderately fast by vigorous undulations of their stumpy bodies, but this looks and probably is an exhausting process. Once in mid-water they can plane down gracefully with outstretched pectoral fins, but on the whole they do not swim much, spending the greater part of their time resting quietly on the bottom. The paired fins are used for walking; the pelvics by virtue of their position under the widest part of the head raise the fish off the ground; they are used as legs and are assisted by the pectorals pushing against the ground. The centre of gravity lies between the insertions of the pectorals and the pelvics. When the angler-fish settles down in sand or sandy gravel it digs for itself a small hollow to accommodate the deep rounded underparts of head and abdomen. The pelvics shovel the sand and any pebbles somewhat forwards and outwards and the pectorals push this material away to either side. The fish has remarkable control over the movements of the pectorals, they are used almost like webbed hands. In a few minutes the hollow is made and the angler then backs into it. One or both of the pectorals may flick a few grains of sand over the back. As the fish finally settles down it slightly raises the head and then lowers it rather smartly. By this action water is driven out from under the fish and, flowing away on all sides, spreads out the irregular tags of skin that fringe the lower jaw and sides of the body. The tags then settle neatly on the surface of the sand alongside. At the same time the pectorals spread themselves flat over the ground. In this position the coloured upper surface of the angler-fish is almost flush with the surrounding surface.

The angler-fish has very perfect powers of matching its colour and colour mottlings to the sand or gravel on which it is resting. I consider that once it has settled down and become fully colour-adapted it is more difficult to detect than the average flat-fish, unless the latter happens to be partially buried. Frequently I have been surprised at the time it has taken to discover the whereabouts, in a not very large tank, of an angler-fish known to be there. The disguise produced by the remarkable way in which the colour mottlings take on the tone and texture of the ground is heightened by the presence of the fringing tags, which break up the outline of the body and merge it most effectively with the surroundings (see Plate I).

When an angler-fish is really settled small bottom organisms crawling over it do not seem to cause disturbance. An *Aphrodite aculeata* has been seen to crawl rapidly across the head and eyes without the fish taking any apparent notice.

Certain individual angler-fishes would sometimes sit propped up among the rocks at one end of their tank. It may be that they were attracted by the small fishes (blennies, wrasses) that tended to congregate there, and the habit does at any rate suggest that from time to time they would naturally haunt rocky places in the sea. The suggestion made by some writers that an angler-fish simulates an irregular lump of rock with the tags resembling attached sedentary organisms should not therefore be dismissed too lightly. I am of the impression, however, that in such a position an angler is more readily perceived by other fishes, but the point is one that is difficult of proof.

Respiration.

A peculiarity of the angler-fish and its relatives is the position of the gill-slit, which opens behind the pectoral fins instead of in front of them as in all other fishes. Viewed from above the slits are largely hidden by the pectoral fins, but their innermost and posterior corners open in the axils between these fins and the trunk. In the position in which the angler normally lies, the lower border of each slit is formed by a loose flap of skin, which in the above-mentioned axil is developed to form a somewhat spout-like structure, or perhaps a better comparison is to the lip of a jug turned upwards. The upper part of the slit is formed partly by the base of the pectoral, and partly by a loose flap of skin, lying in the axil, and stretching from the fin to the innermost posterior edge of the slit where it passes into the spout. Except during expiration the spout is covered by this loose dorsal flap of skin and is invisible from above. When expiration takes place the flap is drawn forwards to uncover the spout and with it forms a round hole (see Figure 2 and compare Plate I where the angler is not expiring). The upward curvature of the spout causes the expiratory current to be deflected vertically upwards. The expiratory currents, one from each side, were frequently so strong that the larger angler-fishes disturbed the surface of the water a foot or more above. The vertical deflection ensures that the sand around the lurking angler is undisturbed when it breathes, thus probably reducing to a minimum the chance of detection by its prey.

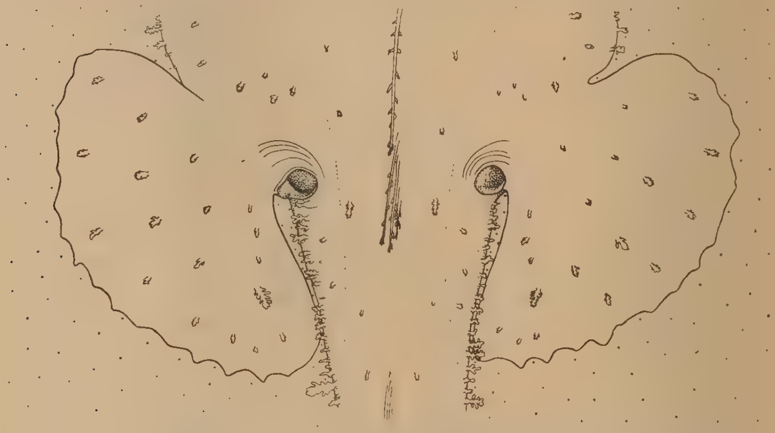

Fig. 2.—A sketch, based on a flashlight photograph, of the gill-slit apertures of an angler-fish during expiration, viewed from above.

When a Lophius is quietly resting there is a long interval between the beginning of one expiration and the next. At a temperature of 11° C. the following times were recorded.

1 minute 25 seconds.
1 ,, 56 ,,
1 ,, 44 ,,
1 ,, 38 ,,
1 minute 50 seconds.
1 ,, 42 ,,
1 ,, 40 ,,

One wonders whether these long intervals may not also assist the fishing, since they enable the angler to keep its body perfectly still while attracting its victims.

A typical respiratory cycle takes place as follows. For most of the period the angler-fish lies still with the mouth closed or nearly so. Towards the end of the period the mouth opens slightly and for some seconds inspiration takes place, the head rising slightly. The mouth is then closed, expiration follows immediately and lasts for a few seconds, the head sinking slowly down again.

While swallowing prey the respiratory rate is increased for several cycles. The resting periods are omitted, and the breathing movements are often more vigorous than usual. Perhaps the swallowing is thereby assisted, or maybe the energy expended in the capture demands an increased rate. On the other hand this increased rate has often accompanied the swallowing of dead fish placed in the mouth and accepted quietly without effort. The movements are genuine inspirations and expirations, not merely discharge of water taken in when catching prey.

Use of the Lure.

There is no doubt whatever that the first dorsal spine, or " rod," with its tag of skin, or " bait "—the whole being known as the " lure "—is used to attract fishes into reach of the mouth. This has not only been seen by Chadwick (1929) and others, but has been repeatedly confirmed by my own observations. An angler when hungry erects the lure immediately any suitable fishes come anywhere near and endeavours to attract one of them close enough to be caught. The lure is quickly jerked to and fro, and as the rod is almost invisible the bait (in my specimens always forked and " fly-like," not vermiform) simulates some tiny creature darting about. An attracted fish rushes up in an endeavour to catch it; the bait is skilfully flicked out of its way just in time and, with a final cast, is dashed down in front of the mouth which may open very slightly. The intended victim, still following the bait, turns slightly head downwards; it is now more or less directly head on to the angler's mouth. The jaws snap faster than the eye can follow, and the tail of the prey is next seen disappearing from sight through the firmly closed mouth.

As far as I have been able to observe the bait is not actually touched by the victim before it is caught, as has sometimes been supposed. Touching the bait with forceps does not cause a reflex snapping of the jaws.

The moving lure has a strong attraction for healthy hungry fishes of several kinds. Small pollack, whiting, pout, and bass were the species actually observed to be attracted to it, but probably most pelagic fish that capture moving prey by sight would at least swim up to investigate the darting object. Many fishes take a ready interest in moving things. A small angler crawling over the bottom of a tank into which it had just been placed aroused, as a rule, the curiosity of nearby fish, pollack and small dabs swimming towards it, keeping, however, at that time a safe distance away.

Besides the quick lashing motion of the lure just described, some anglers occasionally combine with it another movement. Every now and then the rod is depressed until the bait hangs just in front of and rather below the level of the lower jaw. It is then for a few seconds given a curious vibratory movement, after which the sharp flicking is again resumed, the bait being jerked over wide arcs in various directions.

The second to sixth spines of the dorsal fin are more conspicuous when raised than the lure; they generally bear numerous short tags of skin along their whole lengths, but lack special tags at their tips. I suspect, but have not been able definitely to prove, that they are sometimes used as an accessory lure. I have once or twice seen them waved from side to side when fish, which the angler presumably might desire to eat, were too distant for the lure to be readily visible. It seemed at the time that the angler was endeavouring to seize their attention, but unfortunately on these occasions the fish were newly brought in from the sea and were too damaged to behave normally. These spines are often kept raised, although quite still, when no fish are about. In the sea water-movements might gently wave the tags; on a fish swimming up to investigate, the lure proper would be brought into play to manoeuvre it in front of the mouth, the more vigorous motion of the bait now attracting the fish more than the spines, which in any case could be folded back. As a rule they remain erect while the angler is fishing.

The lure is not invariably used when prey is captured. Very often angler-fishes simply sit quite still until a fish chances to swim near enough. They can be very patient. Individuals vary much in this respect, some using the lure much more than others. When the lure is not in use it is depressed right back between the eyes, while the other dorsal spines may or may not be raised. Some individuals were often observed to direct the lure forwards horizontally across the mouth, keeping it quite still in that position for hours on end. Whether this has indicated hunger, and the rod was in a ready position for instant action, I have not been able to determine satisfactorily, but suspect that hunger may have been the explanation.

Angler-fishes rarely chase their prey. Very occasionally I have seen them crawl towards some newly introduced pollack or similar fishes which they had been unable to attract, only to settle themselves down again and ply the lure from a nearer vantage point. If a fish passes a little to one side an angler may turn its head slightly towards it, but never more than the merest trifle. The movement is so slight that I have never seen a fish alarmed by it. To a practised eye the presence or absence of slight movements of the head and eyes, and other almost imperceptible signs, will show whether an angler-fish is hungry and interested in prey or not.

Seizure of Prey.

The actual seizure of the prey takes place too quickly for the human eye to follow. One moment the pollack is there trying to catch the bait, the next the angler-fish is sinking back with the pollack's tail protruding from its jaws. In between there is a blur of rapid movement which defies analysis by straightforward observation. Certain points, however, seem clear and can be stated.

The angler-fish nearly always strikes when the fish is just in front and a little above the level of the mouth. The latter is almost completely closed, although there may be a slight anticipatory gape. The prey should be more or less head on and approaching slowly, although this is not an invariable rule. When the moment comes to strike it seems that the angler suddenly thrusts itself a short way upwards and forwards with the aid of the pelvic fins braced against the ground. Little assistance appears to be given by the pectorals. At the same instant the mouth opens and presumably the buccal cavity is rapidly enlarged, sucking in water and fish at the same time. The jaws snap and the angler sinks back into its sandy hollow to swallow its captive in more leisurely fashion. The tail slowly disappears between the angler's lips, the fish, which always lies on its side, being drawn in and swallowed head first. The heavy breathing movements that occur during swallowing have already been described (p. 487). As the still struggling fish passes down the œsophagus and reaches the stomach its captor sometimes shivers a little as at a queer sensation.

It is well known that when the mouth of an angler-fish is closed the lower jaw projects a considerable distance in front of the upper. This leaves a well-marked gap between the two jaws. The gap is closed by a flap, pigmented on its upper surface, which is attached below the rows of lower teeth and projects freely backwards towards the upper jaw behind. This flap among other functions seems to play an important part in preventing the escape of prey, especially when a fish has to be turned in the buccal cavity preparatory to being swallowed head first. When a fish has been caught broadside on, and has not been very firmly held between upper and lower teeth, I have watched this flap gradually and carefully worked over the fish, starting from one end or the middle.

Guitel (1891) suggests that swallowing is assisted by the very mobile superior and inferior pharyngeal teeth, which by a to and fro action drag the prey in through the jaws and pass it back into the throat. This may very well be so ; the point could be investigated with an X-ray apparatus.

The angler-fish always endeavours to seize its prey head first, but is sometimes unsuccessful, especially if it strikes at a fish swimming over it from behind forwards, or one that is crossing the jaws at right angles to the body axis. In these circumstances it is quite common for the fish to be seized by the middle of the body, both head and tail projecting from the jaws. The head is usually drawn in first, not without difficulty as the angler's hold must be loosened an instant and there is a chance of the prey escaping. Occasionally the fish may be caught tail first, leaving the head projecting ; this is drawn in—one or two careful gulps may be necessary—and I believe, but cannot be sure, that on such an occasion the fish is turned round within the buccal cavity so as to be swallowed head first.

The few flat-fishes I have seen taken were always caught head first as they were approaching from directly in front. My impression is that greater care is taken to seize flat-fishes in this way and that they are not as much esteemed as round fishes. On one occasion when a small dab was lying across its mouth an angler-fish struck at a young whiting. The whiting was caught by the middle of the body, but in the action the dab was sucked in through the mouth. The presence of the dab obviously disconcerted the angler which seemingly tried to swallow it first while still holding the whiting. After some seconds, however, it released the latter and swallowed the dab, several pronounced gulps being required to get it down. The whiting was caught and swallowed a few minutes later, after which no further interest was shown in food.

The incident just related was the only occasion on which I have seen more than one fish caught simultaneously. I believe that an angler-fish takes care, as a rule, that not more than one shall be seized at once, especially if the fishes be of a fair size relative to itself. It seems too that a captured fish must be completely swallowed before the angler is ready to strike again.

An angler-fish rarely misses ; only once or twice have I seen it happen, the intended victim dashing off in great alarm. An angler does not strike unless capture is a reasonable certainty. Once or twice an angler-fish has released a well-caught fish, probably because it was too large and struggled too violently for it to be swallowed in comfort, the angler perhaps not being extremely hungry at the time.

Amount of Food taken at one Meal.

Lophius has long had a reputation for gluttony that seems to be based only on the size of its mouth, an occasional well-filled stomach, and on the fact that fishes are often found in its buccal cavity when the trawl is hauled. These latter, at any rate, almost certainly got there by accident, for should an angler, in its struggles amid the densely packed cod-end, happen to open its mouth an assortment of creatures will immediately fall through the gape and it will be almost impossible to eject them. Some, indeed, the angler may even be forced to swallow.

In captivity an angler is no more gluttonous than any other fish, and perhaps less so than some. The number of fishes it will take at a meal varies, of course, with their size and the hunger of the angler. Generally speaking an angler that has been feeding regularly will take one or two, occasionally even three, round fishes such as pollack when they are about equal in length to the width of its mouth. It will then refuse food for two or three days, when it is again ready for a meal. It seems to take about two days for the stomach to empty itself of one meal and prepare for the next. Quite often an angler that has been induced to take food on the day following a meal has been sick a few hours afterwards, frequently during the night. The partially digested remains of both meals have been readily distinguishable, one meal being more macerated than the other.

Size of the Fishes taken.

It was quite evident from my observations that the captive angler-fishes much preferred their prey to be on the relatively small side. Out of a number of different sized pollack they would definitely try to select those shorter than the widths of their mouths, and would regularly refuse to strike at those which well exceeded these widths, even though hungry and given excellent chances of catching them. Quite often I have seen a relatively large pollack hover in perfect safety close above an angler's mouth, although a little later smaller fish of the same species would be eaten. In general it can be stated that a fish as long as an angler's mouth is wide is the maximum size normally taken. Very occasionally I have watched an angler swallow a fish larger than this, and no doubt they will take such when more than ordinarily hungry. On the other hand, it is already recorded how angler-fishes will sometimes release large and powerful fish they have seized (see p. 490). There is no question that the act of releasing was always deliberate on the part of the captor ; it always had a good and powerful grip on the prey.

These observations accord with Fulton's remark that " the great majority of the fishes found in the stomachs were small even when the angler was large." Now and again relatively very large fishes are found in the stomachs of angler-fishes : perhaps a really ravenous angler will strike at prey larger than usual, and no doubt individuals vary to some extent in their prejudices as regards size.

SPECIES EATEN.

The angler-fish shows distinct preferences for certain types of fish. There is little doubt that it will eat readily soft-finned round fishes such as pollack, whiting, pout, grey mullet, and clupeoids, while on the whole avoiding species with strong spines or of unusual shapes. A small shoal of gadoids or of clupeoids (such as a bucketful of " brit ") released in its tank instantly evokes excitement and interest, whereas wrasses, sticklebacks, and flat-fishes have in my experience failed to arouse this response. As mentioned previously, flat-fishes are swallowed, but only, I think, when the angler is really hungry and other species are not available—at least this is true for the small angler-fishes I have kept. I have never seen a wrasse fished for or caught, although there is some slight evidence that occasionally they have been taken when no observer was present. On the other hand, dead wrasses, both *Ctenolabrus rupestris* (L.) and *Labrus bergylta* Ascanius, have been repeatedly fed by hand to several young angler-fishes. The slow and hesitating manner in which these and other dead fishes were usually swallowed was in marked contrast to the quick certainty with which naturally seized living fish were dispatched.

Some species have been repeatedly refused; these were *Agonus cataphractus* (L.), *Trigla hirundo* Bloch, *Spinachia vulgaris* Flem., and *Syngnathus acus* L. Several times a suitably sized gurnard has given more than one angler-fish several excellent opportunities to catch it. Once or twice as it was passing within easy reach an angler has made to strike and then hesitated. It was reported to me by witnesses that one angler-fish did seize a gurnard swimming over it amid a shoal of pollack, but that it released it immediately. I once saw a fifteen-spined stickleback caught twice in succession and each time released, the angler-fish taking no further interest in it. The stickleback continued to live in the angler's tank for seven weeks afterwards ; it showed no signs of damage, and doubtless owed its life to its hard protective coverings and the stiffness of its body. The same angler regularly swallowed considerably larger pollack.

In addition to the species already mentioned as being readily eaten by my angler-fishes some others were taken from time to time. Chief among these were gobies, *Gobius minutus* Pallas certainly, and possibly also *G. paganellus* L. The shanny, *Blennius pholis* L., was caught once or twice, and on one occasion a Lesser Weever, *Trachinus vipera* Cuv. & Val., was swallowed without ill effect. It happened by accident ; the angler in question was lying in wait for a small shoal of pollack and whiting living in the tank into which it had just been put for feeding purposes. These fish were passing close by, but just out of reach, when a net, accidentally dropped into the tank, hit a buried weever some distance away. The weever dashed off in a direction heading for the angler's mouth, approaching from in front; it was seized with amazing speed and immediately swallowed head first, its struggling tail protruding for a few seconds. The angler-fish seemed to suffer no inconvenience from the weever's poison spines and duly digested it before taking further food.

Bass occupy an anomalous position in the dietary of my angler-fishes. There was a shoal of small ones in the feeding tank at a time (January, 1936) when I had two angler-fishes in perfect health. One (No. 2) was about 17½ inches long; the other (No. 4) was about 11½ inches long. The bass were roughly half the length of the maximum sized pollack No. 4 was taking and were therefore suitably sized prey for both. The larger angler would catch and swallow them readily whenever it was given the chance, but the smaller persistently refused to strike at them. On several occasions when the bass were attracted to its bait, and hovered around its mouth in easy position for capture, this angler-fish deliberately folded back the lure into the position of rest and would not resume fishing until they had wandered away. It was quite evident that this angler preferred the pollack also present in the tank, and that it did not want the bass. Had the spiny fins of the bass anything to do with this, and would this angler have eaten the bass had they been still smaller? We can only guess. Guitel, however, records that his angler-fish ate a bass half its own length: was his desperately hungry?

Fulton (1903) has examined and analysed the stomach contents of five hundred and forty-one angler-fishes caught mainly in the Moray Firth, Aberdeen Bay, and off the Shetlands. Nearly half the stomachs were empty and were "shrunken and collapsed, with thick walls, probably showing that a considerable interval had elapsed since a meal had been obtained." The remaining half contained mostly the remains of fishes with a small admixture of cephalopods and crustaceans. Of the fishes about seventy per cent were round fishes, mainly whitings, haddocks, codlings, sand-eels, and herrings with an occasional Agonus, gurnard, lesser weever, Norway pout, and Lumpenus. Flat-fishes comprised roughly thirty per cent of the fish food and of these common dabs were by far the most numerous, solenettes, long rough dabs, plaice and flounders being also eaten. It will be seen that these observations on the stomach contents of anglers caught in the sea agree closely with the conclusions arrived at from the study of living anglers in captivity.

There are fairly frequent records in the literature of sea-birds having been swallowed by angler-fishes. The indications are that the birds are seized on the surface, the anglers coming up below them. Whilst it does not seem usual for angler-fishes to go after their prey in this way they may so behave when very hungry.

SOME REACTIONS OF FISHES TO THE PRESENCE OF AN ANGLER.

When living fishes are put into a tank containing an angler-fish they do not immediately become aware of its presence, and the same remark applies when an angler-fish has been induced to settle down in a tank containing fishes fully acclimatized to that tank. Bottom fishes such as dabs and gurnards have several times been seen resting on an angler-fish large enough to swallow them, sometimes even lying across the mouth without showing awareness of danger. Small pollack have accidentally touched an angler's soft body and not shown signs that they were aware of its nature. In the ordinary way fish rarely or never perceive the angler once it has merged itself with the bottom as already described (p. 485). Even when one of the members of a small shoal of pollack had been attracted away and caught close-by, its companions gave no indications of alarm.

After some time in the tank of the angler, a fish that has not been caught will gradually become aware of the danger to which it is exposed and will then keep well out of reach. Small pout and pollack have survived thus for several weeks until one day, while less wary than usual, or when upset by a sudden fright, they have swum too near and been eaten. Fish aware of an angler are not attracted by its lure. Small pout, wrasses and blennies would circle round food dropped on an angler's back, always keeping at a respectful distance. Food dropped well away from the angler would be rushed for at once, but only once or twice has a rather large wrasse been so bold as to sneak up behind and take food from the back of the angler, and then only from a part some distance from the mouth.

Fish therefore can learn to avoid an angler-fish, but whether they do so in the sea is a matter for speculation. Fulton (1903, p. 199) seems to think that they may: his opinion is that "the rarity of the large fishes in the stomach of the angler probably points to their greater caution than when younger. Experience, no doubt, teaches them more readily to detect and to avoid the formidable lurking trap which forms part of their natural environment." While this may be true it may also be due partly, perhaps mainly, to the angler's habit of avoiding, as a rule, the capture of relatively large prey.

REGENERATION OF THE LURE.

The lure is of such prime importance to an angler-fish that its loss might be attended with serious consequences. Aristotle has remarked on the thin state of anglers that had lost their baits. It is a delicate organ and easily damaged. No doubt it is not essential and an angler-fish might still be able to capture stray fish that chanced to wander near, but in a sparsely populated region this might not occur sufficiently often to keep it well fed. If it is lost, can it be replaced?

I have good reason to believe that this is so. When, a month after its arrival, my first angler-fish was carefully compared side by side with another of exactly the same size freshly caught but dead, it seemed evident that the former's lure was missing. The organ was present and easily seen in the dead specimen, but could not be found in the living fish, although the knob on which it should articulate was clearly present in front of the true second spine. Thereafter, watch was kept for any sign of regeneration. For about the next four weeks, when the fish was kept in a shallow bowl, a careful and almost daily examination was made in a good light, but nothing rod-like was seen. At the end of this period the angler was placed in a small glass-fronted tank in the public part of the aquarium and it was there difficult to observe fine anatomical details with certainty. During the last fortnight before it died close observation was not made, but two days before death attention was attracted by what appeared to be a tuft of fine skin or mucus which seemed to be attached to the skin on the inner side of the right eye ; this had not previously been seen. On removing the fish from the tank after death it was at once obvious that this tuft was none other than a well-formed bait on the top of a fishing rod normal in appearance. The conclusion reached was that the lure had been regenerated—assuming that previously it had had one and lost it in the sea or in the trawl—while the angler-fish had been living in the aquarium tank.

SUMMARY.

1. Young angler-fishes have been kept alive and in health for periods varying from a few weeks to eleven months. They were sometimes hand-fed on dead fishes and sometimes allowed to catch living prey. They grew at an average rate of about eight and a half inches per annum. All had strongly marked individual characters.

2. With pelvic and pectoral fins a slight hollow is made in the sand into which the angler settles itself. Its upper surface is now flush with the ground, and the colour and colour mottlings are closely matched to the surroundings. The bordering tags of skin break up the outline.

3. Breathing movements occur at relatively long intervals. The expiratory currents are discharged in the axils between the pectoral fins and the trunk, and are deflected vertically upwards.

4. When fishing the lure is jerked smartly in all directions. Small fishes are snapped up, one at a time, as they try to catch the bait. They are generally seized and swallowed head first. The second to sixth dorsal spines and their tags possibly function as secondary lures when attracting fish from a distance.

5. The angler-fishes usually fed every two or three days. The largest sized fish taken was, as a rule, as long as the angler's mouth was wide. One or two such fishes would form a meal.

6. Angler-fishes appear to prefer gadoids, clupeoids, and similar soft-finned round fishes to any others. They will eat flat-fishes, but not so eagerly.

7. A lurking angler is not readily detected by other fish. In time, if they are not caught, they become aware of its presence in their tank and keep away.

8. If the lure is lost there is evidence that it is regenerated.

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EXPLANATION OF PLATE I.

Photograph of an Angler-fish (*Lophius piscatorius* L.), 7¾ inches long, resting on the bottom of its tank and fully colour-adapted to its surroundings. It had dug for itself a slight hollow in the sandy gravel and was known to stay in this place for at least six hours. The lure is held forwards, the rod crossing the mouth horizontally. The divided bait, dark in tone, is clearly visible at the middle point of the lower jaw, between it and the light-toned piece of gravel to the right of the umbo of the Nassa shell. The lure is being held perfectly still; no fish are in sight. The second to sixth dorsal spines are depressed.

Technical data: One magnesium flash on the right side. Ilford Soft Gradation Panchromatic plate. No filter. f/44. Taken through the surface of the water: depth about fourteen inches.

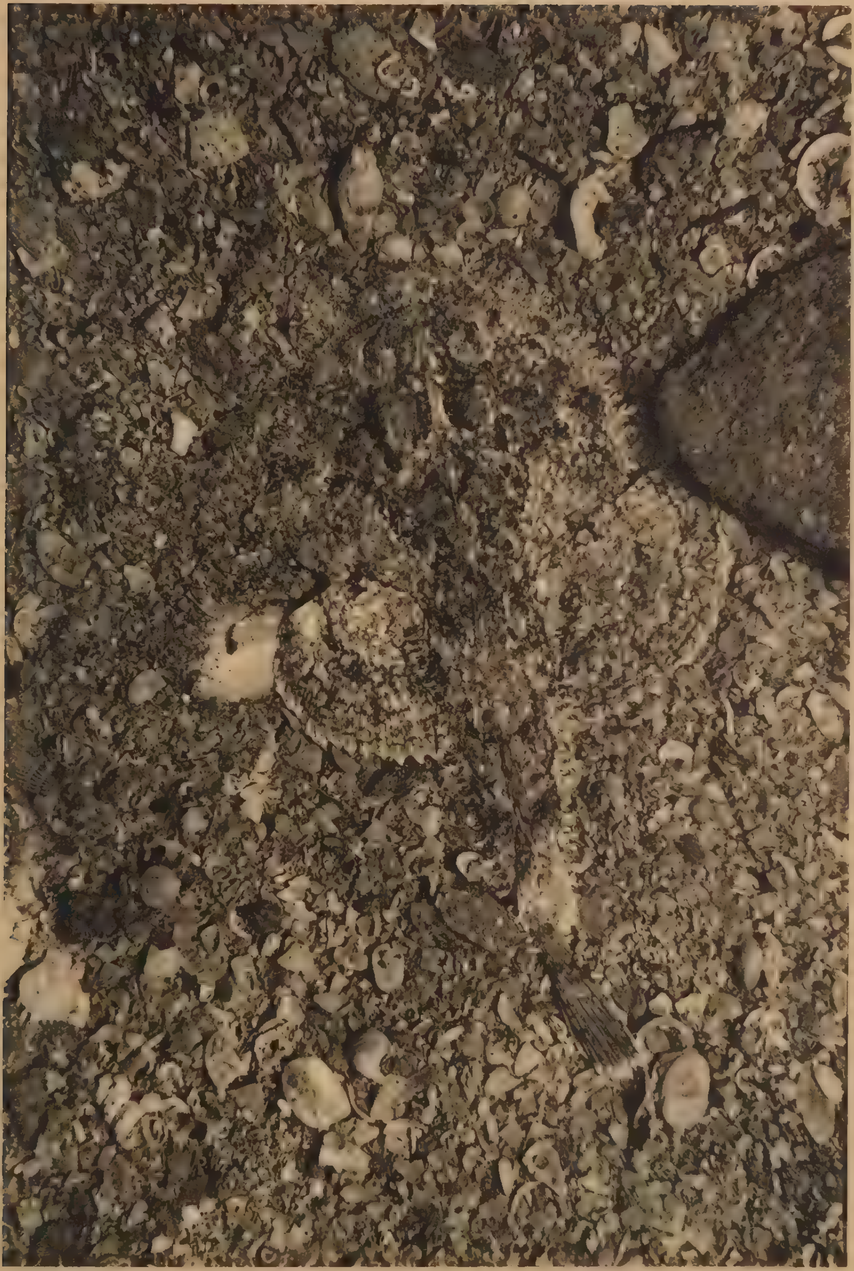

Photo. D.P. Wilson

John Bale Sons & Danielsson L^{td} London.

To face page 496.

The Learning of Detours by Wrasse (*Ctenolabrus rupestris* L.).

By
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With 13 Figures in the Text.

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PREFATORY.

THERE is probably no branch of biological research which can continue indefinitely without finding itself compelled to take account of the specific behaviour, if not actually the psychology, of the organisms with which it deals. This necessity has already been noticeable even in those departments of study in which attention is concentrated on the more abstract features of organisms, and in which individuals are regarded, as far as it can possibly be managed, as units of a standard type, acted on by independent external forces. No better illustration can be found than the attempts at relating the phenomena of organic structure to the causal agency of natural selection. If further light is to be thrown on this fundamental problem, no subjects are more suitable for the purpose than sexual selection and mimicry. But in both these fields of investigation progress is arrested until considerably more is known of the behaviour of the animals concerned—in the former, of the actual effect which display of sexual structures exerts on choice of mates, or stimulation of coition ; in the latter, the whole problem depends on the extent to which the mimetic characters can serve to impose on the sensory discrimination of predators. Lloyd Morgan (1900, p. 311) was one of the first to appreciate how the situation was developing. " Many interesting problems," he wrote, " which are keenly discussed by evolutionists in the light of natural selection presuppose conscious situations which are more or less tacitly taken for granted." Of course, stress need not be laid on the expression " conscious " : it is sufficient for the point at issue to put " discrimination responses " in place of " conscious situations."

If behaviour cannot be ignored in the morphological sphere, still less is this possible in the ecological, when problems concerning the distribution of populations, and of relations of individuals to their physical and biotic surroundings, are encountered.

There are two rather different ways in which behaviour characteristics come increasingly to force themselves on the attention of ecologists.

(i) The fixed and regular aspects of behaviour of which account has to be taken, or which at least have to be assumed or are presupposed, may take on an intricate and specific form requiring elucidation by special study. As a clear illustration from animal ecology, one may cite the significance of the factor of " habitat selection " in interpreting the causes of distribution of breeding birds in an area of mixed habitats, as recently shown by Lack (1933). In marine biology similar cases come to notice. The vertical distribution of populations of plankton organisms is evidently to a large extent dependent on the specific behaviour reactions of the animals to the illumination of the water, or other factors in their environment. The availability of food for, e.g. bottom-living fishes, or shore birds, seems to depend more than at first might be expected on the special methods (due to specific feeding reactions) the animals employ to obtain it ; so that the *setting* of the food organisms has to be taken into account, in addition to their mere *presence*. To quote one other familiar example —the breeding migrations of many fish are unquestionably regulated by special instinctive responses, and until something more is known about these the whole study concerned with the factors which affect the movements of populations of these species can scarcely progress far.

(ii) Secondly, it may come about that it is insufficient to regard only the fixed and regular aspects of behaviour, but that account has to be taken of the fact that the behaviour of both individuals and communities is modifiable, and, within limits, capable of adaptive, or even progressive, change. It seems that most ecological problems which have to take concern of special features of behaviour are destined to come up against the complicating factor of the *modifiability* of behaviour. Even in the case of the vertical distribution of plankton the effects of physiological adaptation to optical stimulation have to be taken into account, significant shifts in the level of maximum concentration being attributable to this factor (F. S. Russell, 1931, pp. 400–405). In vertebrates this aspect can probably never be ignored for long. The return migration of fish to their breeding grounds, in so far as it is dependent on reactions to environmental stimuli, appears to involve reactions conditioned by the past reactions of the fish. At least there is evidence that this is so in the case of the Pacific Salmon (Rich and Holmes, 1928).

Again, the diets of shore and estuarine birds, some of which can utilize a considerable variety of food organisms, may vary according to the birds' acquired habits. It is a familiar fact that birds may ignore an unfamiliar source of food until discovering it by chance, when subsequently they may take heavy toll of it. This may happen, in the case of shore birds, to an extent sufficient to affect appreciably the mortality of shore invertebrates, and so once again the modifiable aspect of behaviour (of predators) has to be reckoned with, in the study of such a comparatively abstract property (of the food organisms) as the rate of mortality.

Another illustration which has recently come to notice shows the intricate relation between ecology and animal behaviour. The distribution of the Great Grey Seal (*Halichoerus grypus*) population in the South-Western area of England is intimately related to the presence of suitable breeding quarters (Steven, 1936). But whereas in the Scillies the seals lay their pups on open beaches, on the mainland of Cornwall they breed entirely in the interior of caves. Whatever has been the cause of this choice (and it probably resides in the attacks on the stock made in the past by man), it is evident that an acquired habit, or behaviour modification, has to be reckoned with. Since the areas which provide suitable breeding caves are severely limited, and the effect of this limitation is reflected on the distribution of the seal population—for instance, causing an almost complete absence on the south coast—the distribution, therefore, is directly affected by this acquired habit of the Cornwall seals.

These examples may serve to indicate how ecological investigations which primarily deal with the most general aspects of some animal population come to be concerned, firstly, with special features of the animal's behaviour, and, secondly, with the *modifiability of that behaviour.* The second aspect opens up an interesting field for investigation, and it is taken as a starting-point for a line of research of which the present paper is offered as a first contribution.

Viewed on a broad scale, all biological study is seen to have its origin in the observations made on organisms in their environmental setting and in the problems thereby raised. It is not complete until the results of the train of research so instigated are directed back to the observations which provided the starting-point. Unless its direction is adequately orientated with respect to this main circuit, laboratory research is apt to narrow in scope, to settle in water-tight compartments, to become too unnecessarily abstract. We have seen that the problem of the modifiability of behaviour is raised in purely ecological studies, which circumstance at once draws it out from its recess among subjects of predominantly academic interest and brings it within the province of action of the marine zoologist. If any justification is required for research on the subject of the modifiability of behaviour, it is the above consideration on which main emphasis is to be laid. At the same time the claims are not to be overlooked of the intrinsic interest of the subject itself ; of its bearing on academic problems such as the evolution of intelligence ; of its relation to the subject of development and maturation ; of the contribution it can make to the interpretation of learning, and the contacts thus established with general biological theory ; and, lastly, of the problems it raises, and should assist in solving, with regard to methods and technique —as yet imperfectly developed—appropriate in the investigation of behaviour.

DETOUR EXPERIMENTS WITH TELEOST FISH.

With a view to making some contribution to the study of the modifiability of behaviour in Teleost fish, it was decided to utilize the method known as " detour " training as a basis for experimental work. The value of this method has been pointed out by E. S. Russell (1931) who, applying a technique made familiar by Köhler in his classical work on chimpanzees, undertook experiments with the freshwater stickleback (Gasterosteus). The capacity of the fish was tested for reaching a food object by a roundabout path. The food, presented inside a glass pot, was easily visible through the glass, but could only be reached if the fish made a detour round through the opening of the pot. At the start the fish attempt to reach the food directly, and may spend a long time swimming at the pot before eventually finding the opening by chance ; but after continued repetition they come to acquire the habit of swimming straight to the opening. In the same way they come to adopt an efficient method of escaping from the pot, an action which at first presents difficulties.

We have evidently here to deal with a behaviour modification of an adaptive type which may be placed in the category of " learning," if this term is used in a fairly general sense. The animal " learns " to develop a response which enables it to overcome an obstruction in its path to a food-object, which functions as the immediate " goal " of its activities. The acquired efficient response has to grow out of several discrete movements, which are at first given independently of each other.

The main problem is to discover how this change in behaviour, this development of a more efficient response, is to be interpreted: what, in fact, are the necessary conditions for its occurrence, and how it is related to the fish's neural organization. The state of the theory of learning in general is such that there is no ready interpretation of the phenomenon. The " learning " of detours is actually a simple form of maze-learning, and presents many features in common with that shown in " puzzle-box " situations, in which the learned response involves the performance of certain movements in a correct order. It is noteworthy that neither in maze-learning, nor in other kinds of problem-solving, does present knowledge extend far enough to make possible an adequate interpretation of the learning process. On the one hand straightforward accounts in physiological terms of a strictly mechanistic type cannot absorb all the facts; on the other hand a theory, such as that of the " gestalt," which majestically ranges over the facts, travels too far beyond those at present available, and, further, is too comprehensive even to have acquired a precise formulation.

The difficulty is augmented by the fact that most of our existing information on problem-learning is derived from higher vertebrates which, it might be said, exhibit the phenomenon in too complex a form. We require to know more of the behaviour of vertebrates lower in the scale which are capable only of the elementary types of problem-learning. With such animals—and here it is that Teleost fish come in—simple situations can be presented which allow of adequate experimental control.

Russell's experiments were carried far enough to give some suggestive indications (1931, p. 408). He established the fact that the fish are normally able to learn simple detours; that the correct solution was first found by chance, and that at first the activity of the fish is undirected, at least in respect to the obstruction; that change in behaviour occurs with repetition of the trials, marked by a change from undirected to directed activity, and by a sudden fall in the learning curve; and that, associated with the acquirement of the efficient response, the pot appears to acquire some sort of significance from the aspect of the fish, as though some change in sensory organization had occurred.

But the question still remains—how did the performance of the correct movements, at first brought about accidentally, become " stamped in " ? The suggestion is implied that it comes about as a result of change of sensory organization, of which the fish's reactions to the pot itself give evidence. The fish comes to sense a certain relation between objects in its surroundings, and adjusts its movements accordingly. This is in harmony with the " gestalt " viewpoint. But there is no claim that the experiments are adequate to serve the difficult function of demonstrating the validity of this interpretation. Nevertheless, the results can perhaps be said to be suggestive ; and it should be realised that if this interpretation of detour learning can, by further experiment, be shown to hold, a considerable step forward will have been made in the study of the sensory capacities of lower vertebrates.

The experiments described below aimed at procuring detailed observations on the fish over the whole course of training, in order to find what relations could be established between the final learned response and the various behaviour reactions given in earlier stages. For instance, it was important to enquire how far successful *methods* of making the detour, perhaps at first arrived at fortuitously, determined the method by which the learned response was performed. Again, were there, it was asked, any features of behaviour in earlier trials which determined whether a learned response would be established or not ? The simplest type of detour was chosen and a record kept of all movements of the fish against a time scale throughout the trial. The records were subsequently subjected to analysis, and, where possible, quantitative data were abstracted. The main features which emerged are discussed in the second half of this paper, after the experiments have been described. It may be noted that the procedure adopted in this investigation resembles somewhat that of the field naturalist, who first sets out to record as minutely and impartially as possible the behaviour, whatever it may be, shown by an animal under observation, and subsequently works out the most important features of the mass of details as a whole ; rather than that of the experimentalist, tackling a clear-cut problem, who arranges his experimental conditions so that a definite answer is given one way or the other. In elaboration of these experiments it should be possible to harmonize the best of both methods.

METHODS.

General procedure. The fish used in these experiments were small, immature specimens of the Rock Wrasse (*Ctenolabrus rupestris* L.), from 5 to 7 cm. in length. This species readily adapts itself to captivity and lives well in tanks of restricted size. It soon gets over the effects of any shock that may be induced by capture in a net or disturbance of its tank. Altogether the species proves an excellent experimental animal.

For the whole of the time during which it was subjected to experiment, each fish was kept isolated in a rectangular glass dish (size either 42 × 24 × 12 cm. or 36 × 28 × 15 cm., internal dimensions). Preliminary experiments were made on three fish (A, B, and C) in the early part of 1934, in two dishes set up inside a larger tank (in the main laboratory) screened from excessive light. The remaining nine fish (D1 to 9) investigated together in the later months of that year were kept in a darkened room, the dishes ($36 \times 28 \times 15$) lying in a row on a long table, screened from each other with strips of cardboard. The dishes were provided with air circulation.

The fish, in each case, was allowed to get thoroughly accustomed to its surroundings, and to take food off a piece of thin wire. After being placed in the experimental dish it was never fed in any other manner. Prior to the feeding an electric light of moderate intensity was switched on. In the main experiment the lighting of the room served as a signal—and probably actually acquired this association—that feeding was about to take place. It was found that the fish very soon came readily to associate the wire with food and gave positive reactions to the observer when he approached the dish. They followed movements of the hand when this was passed over the tank, and also were closely attracted to the pipette used from time to time for picking up debris accumulated in the dish. Any shock reactions given at first soon disappeared, and they soon became indifferent to such extraneous stimuli as may have reached them (e.g. vibration from footsteps in neighbouring passages). These facts are emphasized to show that feeding responses, at least, were free from inhibitions which might have interfered with the experiments.

After an adequate period had been allowed the fish for settling down, experimental feedings were started. The fish now never fed except in a situation in which it had to surmount a certain obstruction: it now always had to take an indirect route to reach the food. Whatever type of obstruction was used the procedure at each feeding followed along the same lines. The fish was enticed to a particular corner of the dish, and at the same time the obstruction (in most cases the arrangement of glass plates described below) was carefully lowered into the tank. The food, still presented at the end of a thin wire, was then transferred to an appropriate position, and left hanging in the water on its wire support. The fish was able to detect the food by sight, but was in such a position that it could not directly reach it. Actually, it had either to enter a pot or pass round a glass plate. A stopwatch was set going as soon as the fish began to swim towards the food, and a record of the observed movements of the fish was taken. The observer's head and shoulders were in the fish's range of view, but it was found that the fish was too absorbed in its attempts at reaching the food to be affected even by quite considerable movements on the part of the observer. For precautionary measures, however, the observer kept still all through the trial, as nearly as possible in the same relative position with respect to the dish. As soon as the food was taken, the obstruction was removed, and the fish once more left in a clear tank. Two such feedings, on an average, were given to each fish in one day. After a time it was possible to reduce the amount of food given at each trial to a very small quantity, so that as many as five feedings could be given in one day before the food ceased to attract.

The food, for the most part, consisted of the muscle of freshly killed prawns. This was now and again varied with small pieces of squid.

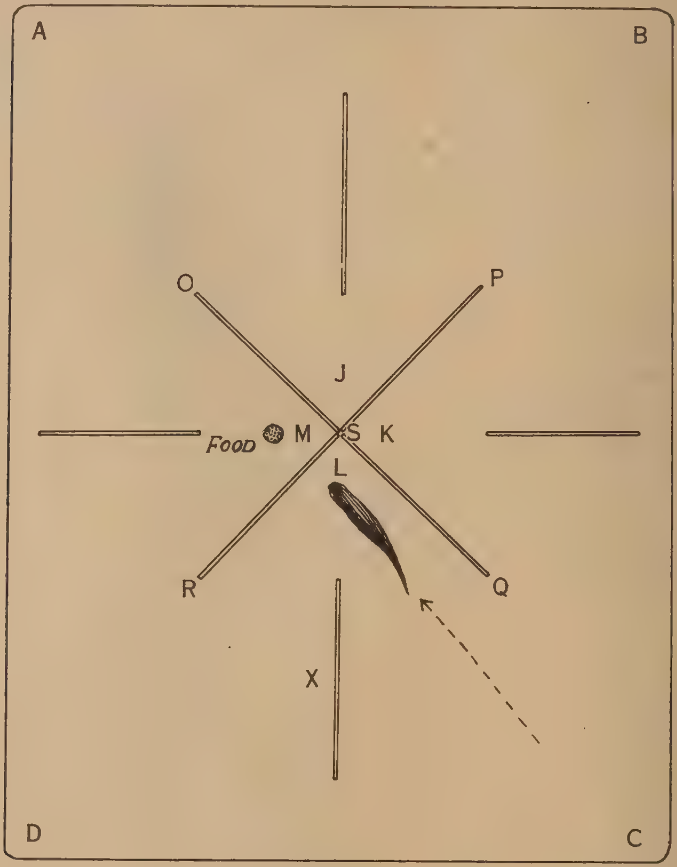

Fig. 1.—Diagram of the arrangement of glass plates used in training the fish. See text, p. 505. ×⅓.

A, B, C, D marks the inner edge of the glass dish. J, K, L, M, S, and X are positions to which special reference is made in the accounts of the experiments. O, P, Q and R mark the positions of the edges of the four central radiating glass plates.

Apparatus. The only special apparatus that requires description is that employed to furnish the fish with a detour path. In the majority of experiments here described it consisted of a special arrangement of glass plates (the glass 2 mm. thick) set in a pattern shown in Fig. 1. These plates were held in a wooden frame made to fit over the top of the dish (Fig. 2). At each feeding the loaded frame was lowered into the dish, the glass plates then forming a sort of maze restricting the directions in which the fish could freely move. In Fig. 1 a number of positions in the horizontal plane are marked by letters, and it will be convenient to use this lettering for describing positions in the dish. The plates OS, PS, QS, and RS were each 8·6 cm. wide. The side plates were fixed so as just to protrude into the square O, P, Q, R.

With this apparatus both the position of the food and the starting position of the fish could be varied in different ways. The symmetrical arrangement of the plates also permitted an easy exchange from right to left, such as is required in testing transfer of learning. In practice, the food (except in the case of fish B) was always placed during training at the position M, and the fish started from the neighbourhood of C. The fish thus had to circumvent the edge R; and in doing this had to make a detour of some 6·5 cm. If the glass plate had a clear surface, or even if its edges were marked with a black line, this simple detour was quite enough to test the fish's capacities to its limits. The other portions of the "maze" served their purpose during tests on fish which had learnt to make a detour of the plate R S.

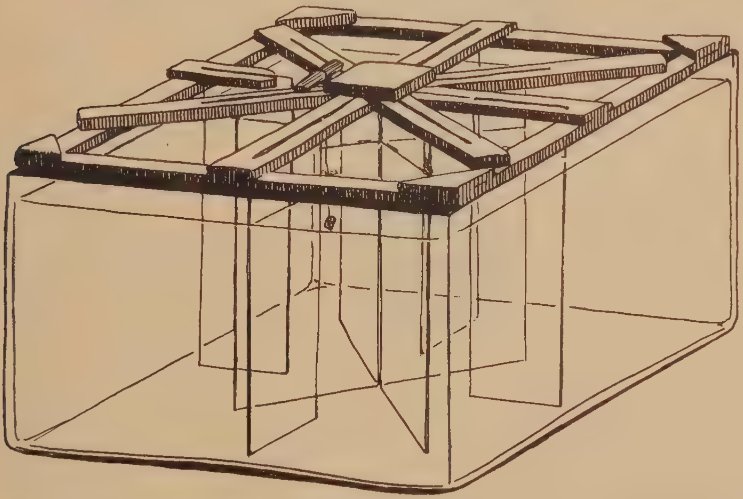

Fig. 2.—Optical view of glass dish with the wooden frame, holding the glass plates, in position. See text, above.

The wire supporting the food was lightly held on a piece of wood resting on the frame in the position shown in Fig. 2. A loop was made in the wire in such a way that the wire fell naturally into a vertical position when placed on the support.

Another piece of apparatus used consisted of a glass tube fixed horizontally on a weighted upright support (Fig. 3). The tube, 10·2 cm. in length, and of 3 cm. internal diameter, had an opening on the side placed uppermost, near the closed end. Through this opening the food, suspended on a wire, was lowered, and thus came to rest inside the tube 8·5 cm. from its open end. The support was painted black and the glass tube covered by a heavy black meshwork, roughly painted on. The extent of the tube was thus made visibly conspicuous, though the food could still be seen through the meshes. The fish could not reach the food except by passing through the open end of the tube.

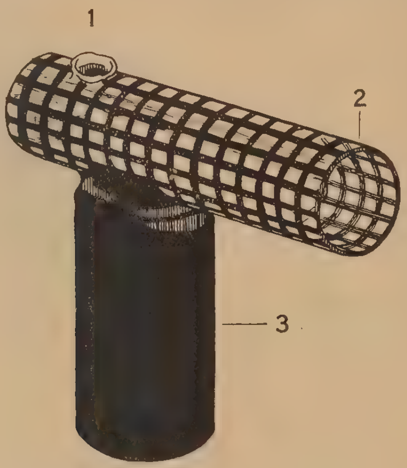

Fig. 3.—Sketch showing the tube, painted with black meshwork, presented to fish D9. See text. $\times \frac{2}{3}$.
1. Hole through which food wire was inserted.
2. Mouth of tube. 3. Weighted support.

DESCRIPTION OF EXPERIMENTS.

I. Detours Necessitating Entry into a Glass Receptacle.

E. S. Russell (*loc. cit.*) has adequately demonstrated that fishes are capable of learning to find their way into a pot, either of clear or somewhat opaque glass, whereas their first reactions lead them to attempt to reach the food directly.

An important characteristic of this type of detour experiment is that the obstruction is more or less easily visible and the indirect route can be in some sense "surveyed" by an animal with adequate powers of vision. The possibility is offered that the pot or tube may become viewed as an object, and both the food and the way of access to it sensed in relation to the object as a whole. This evidently happens in the case of higher mammals, and may well happen to a greater or lesser extent in that of teleost fish. Russell found that the fish, after training had progressed, came to give special reactions to the pot itself, as though it had acquired a new significance in their world. This at least indicates that the fish were capable of sensing the pot as an object.

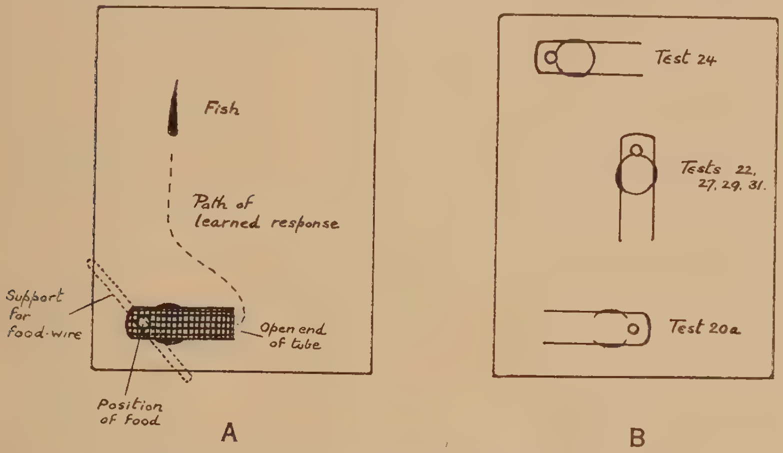

FIG. 4.—Diagrams of conditions presented to fish D9. × $\frac{1}{8}$.
A. General conditions under which training took place. B. Three alternative positions of the tube given in the tests indicated.

Since the wrasse proved capable of learning a more difficult type of detour, more suitable for procuring the type of data required, it was not considered necessary to repeat the pot experiments. One fish, however, was given the meshed tube described on page 506 (Fig. 3). The tube with its black support could not have failed to provide a conspicuous object, and the meshwork marked the glass obstruction in a conspicuous manner.

Fish D9.

Length: 5½ cm.

After 8 days in the dish the fish had settled down and took food readily off the wire. The pot was then introduced (Nov. 23): the fish showed "apprehension" and could not be enticed closer than to 5 cm. of the new object. The pot was removed and replaced the next day. Two feedings were then given (Nov. 24) as close to the pot as the fish would approach, now about 3 cm. The pot was now left in the dish until Nov. 26, when feedings were given both over it and close by its side. The inhibitory influence of the pot was now disappearing. The pot was then left in the dish, and next day it was possible to give the first trial feeding, the pot now having no inhibitory influence at all. Thus the latter was overcome in four days.

For the first day (Nov. 27), when three experimental feedings were given, the pot was left in the dish, but subsequently it was removed after each trial. It was always placed in the same position in the dish near corner D, in the position shown in Fig. 4a.

The fish was attracted to the far side of the tank. The baited wire was then lowered into the hole on the upper side of the tube, and hooked over a wooden support resting on the corner angle of the dish (Fig. 4a). The stop-watch was set going as the fish passed the middle of the dish in the direction of the food.

A modification, however, of this procedure had to be introduced after a dozen trials. The pot, by then, had become such an attraction in itself that the fish now often entered it before there was time to introduce the food at all. So the food was now placed *inside* the tube before the latter was lowered into the tank. It now lay on the bottom of the tube near its closed end, and, incidentally, was now in a more inconspicuous position.

The duration of the trials are given in Table I. These figures serve to indicate the rapidity with which the fish came to develop an efficient performance.

TABLE I.

Fish D9. Duration of Trials.

Date.	*Serial No.*	Duration of trial.	Remarks.
Nov. 27	*1*	7′ 18″	
..	*2*	3′ 04″	
..	*3*	5′ 43″	
28	*4*	2′ 25″	Entered tube a second time.
..	*5*	2′ 18″	Investigated opening before [food introduced.
29	*6*	1′ 59″	
..	*7*	0′ 49″	
..	*8*	(4′ 51″)	Not adequately attracted [by food.
30	*9*	0′ 26″	
Dec. 1	*10*	3′ 05″	
3	*11*	0′ 36″	
..	*12*	1′ 29″	
4	*13*	0′ 32″*	Food now introduced with pot.
5	*14*	0′ 11″*	Efficiency now attained.
..	*15*	0′ 27″*	
..	*16*	0′ 13″*	
6	*17*	0′ 10″*	
..	*18*	0′ 12″*	
Dec. 7	*19*	0′ 11″*	
..	*20*	0′ 14″*	
..	*21*	0′ 16″*	
..	*22*	(Test)	
10	*23*	0′ 14″*	
..	*24*	(Test)	
..	*25*	0′ 14″*	
..	*26*	0′ 08″	
..	*27*	(Test)	
12	*28*	0′ 09″*	
..	*29*	(Test)	
..	*30*	0′ 19″*	
..	*31*	(Test)	
13	*32*	0′ 09″*	
..	*33*	0′ 17″	
..	*34*	0′ 09″*	
..	*35*	0′ 14″	

Any doubts as to whether the pattern on the tube prevented vision of the food inside were quickly dispelled during the first trial. For two periods, each of about $\frac{3}{4}$ minute, the fish made persistent attempts at reaching the food object through spaces between the meshes. It worked actively all round the closed end of the tube. It even snapped at the glass from below. Its behaviour was perhaps remarkable when it is remembered that only two days previously it was still nervous of approaching the pot.

More than seven minutes passed before the fish eventually reached the food in this first trial. After some fruitless efforts at reaching the food directly, it spent some time swimming irregularly around the pot, with occasional excursions into other parts of the dish. But it was a long time before the fish came right opposite the opening of the tube ; for the latter lay rather high in the water and the fish tended to swim at a lower level. It was not until 7′ 13″ that the fish's movements brought it immediately abreast of the opening, and that for the first time could it have had an open view of the food. It would not have been surprising if the fish had now displayed hesitancy. Viewed from the opening, the food had a bizarre visual background of radiating and intersecting black streaks, which may well have obscured the outlines of the food object in the fish's visual field, even if the pattern did not itself exert an inhibitory effect. The fact is, however, that *the fish swam straight into the tube and snapped at the food without the least hesitation.*

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* Food already inside the tube, lying on the bottom, when the tube was lowered into the tank. All trials after *13*, except *18*, *26*, *33*, and *35*.

The next few trials were performed in a similar manner, the fish swimming into the tube the first time it happened to come opposite the opening. It never again took so long as on the first occasion, and would doubtless have given still better results if it had not shown a tendency to swim round underneath the opening.

There were early signs that the fish was beginning to acquire some familiarity with the apparatus in which it was fed. After trial *4* it swam into the opening a second time. At the beginning of *5* it swam up to the mouth and looked inside, before the food was introduced. Again, at the beginning of *6*, it swam up to the opening and inserted its head into the tube. But in both these trials, once the food had been introduced, the fish still persisted for some while in its attempts at reaching the food directly, and took over two minutes to make the detour.

In trial *7* for the first time the fish reached the food in less than a minute. Trial *8* is unsatisfactory, as previous to it the fish had been accidentally disturbed, and when the trial was given it did not appear to be at all strongly attracted to the food. It was still probably in a certain state of inhibition. The length of duration of *10* is to be attributed to disturbing influences. There was some delay in presenting the food, and during this interval the fish swam into the empty pot at least twice on its own "initiative." There was also a second observer present. Apart from these two trials, a reasonably steady improvement in efficiency of performance may be seen.

An important factor in the increase of efficiency was a reduction in the time spent in attempts at reaching the food direct. This suddenly fell to 5″ in trial *9*, and, though the next three trials gave 1′ 30″, 20″, and 36″ respectively, it suddenly became negligible from *13* onwards. From this point the fish no longer spent any time in attempting to reach the food direct through the glass.

Trial *13* marks a point of rather sudden improvement. After this trial an efficient response can be said to have become established. From *14* onwards the fish rarely even swam to the closed end of the tube where the food lay: as it passed towards the tube, at a distance of about

10 cm., it diverted its course somewhat to the left to bring it to the open end.

It is to be noted that this main step in the progress of learning also coincides with a modification in the experimental conditions referred to above—from *13* onwards the food was inside the tube when the latter was placed in the dish. It is possible that this change exerted an effect on the course of learning ; but if it did so, the effect was a favourable one. It is noteworthy that the main difference involved was that the food was made *less* conspicuous—probably invisible except at close quarters—and so may not have held the same attraction as before. It is therefore possible that there was less to distract the fish from its growing tendency to move to the open end of the tube, but if this were so, the fact is certainly noteworthy. If not, then the sudden improvement has to be regarded as an independent feature of the learning process (e.g. as in fish D5, pp. 528, 550).

When the original conditions were repeated (trials *18*, *20*, etc.) there was no difference in the fish's performance from that in other trials.

During the efficient period (*14* onwards) the fish, as has been stated, rarely even visited the closed end of the tube. In the best performances it swam straight to the opening, and in, without hesitation. But it still on occasions swam round the pot once or twice, having missed the opening first time.

Certain tests with the pot placed in different positions were made. The positions are shown in Fig. 4. Thus in trial *20a* the pot was turned round so that its opening faced corner D. The fish took its usual course, swimming straight to the left-hand end (left, that is, from the position of the fish) and made persistent efforts to get into the tube at this point. The trial was abandoned at 1′ 30″. Trial *24* provided a mirror image of the normal situation. The fish again tried the left-hand side first, but this time did not persist in attacking the end : it swam to and fro and reached the food in 37″. Both these tests indicate that the fish had acquired the habit of *moving to the left-hand side of the tube*, whatever its position, rather than to distinguish the open long arm of the tube from the short closed arm.

Four tests were made with the pot standing in the middle of the dish, the opening facing towards the observer. The fish was started on the left-hand side. In the first two (*22*, *27*) the fish swam round and round the tube and did not enter it even when coming abreast of the opening. Both tests were abandoned, after 3′ 30″ and 2′ 15″ respectively. However, both *29* and *31* were solved readily (10″ and 30″). It is possible that the different relation to the electric light, and so a difference in the illumination of the interior of the tube, was responsible for the failure of the first two tests. One can at least conclude that the position of the tube relative to its background and to the angle of approach of the fish was still of importance.

These details of the performances of fish D9 are given to illustrate the type of result obtained with wrasse when the arrangements seem to supply optimum conditions for learning. The obstruction is easily seen, while at the same time the food remains visible; there is only one indirect route, which can probably be readily surveyed by an animal with adequate powers of vision; the task of discovery of the indirect route is well suited to the natural exploratory behaviour of wrasse. It emerges, however, that this type of detour problem is not well suited to the sort of analysis we wish to undertake. The fact that there is really only one method of solving the problem is a severe limitation, and the efficient response is arrived at too rapidly to allow of comparisons between its separate components.

II. Detours necessitating Passage round Partitions of Glass.

With the apparatus described on page 504 it was possible to try out a detour of another type—one in which the obstruction is invisible or only figures very obscurely in the fish's visual field. Other varieties of glass plates can always readily be substituted, such as ones with their surface marked in some way so as to render it conspicuous to the fish. The apparatus also allows of other modifications of experimental procedure and is thus conveniently adaptable.

The results of the preliminary experiments, with fishes A and B, showed that wrasse are capable of learning to get round a plain glass obstruction effectively, although an efficient response is acquired with difficulty and precariously maintained. Fish A was presented with the problem subsequently given to other fish, of group D, but since other conditions differed somewhat, caution must be used in making detailed comparisons between the performances of A and other fish.

The experiments on fishes D1 to 8 were carried out simultaneously under comparable conditions. D2, 3, 4, and 5 were given an obstruction of plain glass, as in the case of A. With D1 and 6 the plate was edged with a black strip, 5 mm. in width. D7 and 8 were presented with a glass plate of similar dimensions, but with its surface marked with a meshwork of scratched lines. The lines on this plate were ruled at 5 mm. intervals, with the aid of a glass-cutter. Though made as firm as possible, and very noticeable in the air, they did not show up very conspicuously under water.

In all these cases, during training, the food was presented at M (Fig. 1), and the fish started from corner C.* A detour of 6·5 cm. to the left had to be made.

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* Except fish B.

Fish A.

Length 6·5 cm.

Jan. 4, placed in experimental dish standing in an empty tank in the main laboratory, under conditions referred to on page 502. For 12 days fed with Mytilus and pieces of Polychaete worm off the end of a wire, until it had become thoroughly habituated to this method of feeding and its conditions in general.

Jan. 16, first experimental feeding. Jan. 16–Feb. 10, 67 experimental feedings given. Feb. 10–14, interval during which fish was moved from the tank and water renewed. Feb. 14–March 3, 67 experimental feedings given. March 4–19, interval during which dishes were disturbed. March 20–22, 11 further experimental feedings.

Trained to plain glass obstruction, detour 6·5 cm.

The experiments on this fish constituted the main part of the preliminary investigations, carried out between January and March, 1934. For the first fortnight there was no indication that the fish was acquiring any increased efficiency in its performance, but eventually it developed a stable learned response, working leftward along the glass until reaching the edge.

The general course of learning is shown graphically in Fig. 5, in which a curve is given representing the duration of successive trials. As is usual with these "learning curves," its course is very irregular until the learned response is stabilized, when it remains at a uniform low level. The averages of groups of five successive normal trials are as follows (trials which are called "tests," in which the conditions are altered in some particular respect are not included in these figures):

Date.	*Serial No. of trials.*	Average duration.	Date.	*Serial No. of trials.*	Average duration.
Jan. 16-18	*A 1–5*	7′ 52″	Feb. 14–16	*B 1–5*	2′ 03″
18–22	*6–10*	5′ 38″	17–19	*6–10*	1′ 17″
22–23	*11–15*	2′ 26″	19–20	*11–15*	0′ 38″
24–25	*16–20*	5′ 03″	20–21	*16–20*	0′ 14″
25–29	*21–25*	6′ 16″	23–24	*24–28*	0′ 16″
30–31	*26–30*	1′ 36″	24–25	*29–33*	0′ 11″
Jan. 31–Feb. 1	*31–35*	1′ 29″	26–28	*34, 43, 44, 48, 49*	0′ 11″
Feb. 1–2	*36–40*	1′ 09″	March 1	*50, 53, 55, 57, 58*	0′ 12″
2–3	*41–45*	0′ 32″	2–5	*59, 62, 64, 65, 66*	0′ 12″
3–5	*46–50*	0′ 37″			
5–6	*51–55*	0′ 31″	March 20–21	*C 1–5*	1′ 02″
7–8	*56–60*	0′ 48″*	21–22	*6–10*	0′ 12″
8–9	*61–65*	0′ 18″			

First series (trials *A1* to *67*). In the early trials the fish found considerable difficulty in reaching the food, and the average duration of the first 24 trials was higher than in any other fish. To start with, there was a conspicuous contrast between two alternating phases of behaviour: the movements were partly directed towards the food, resulting in the fish keeping close to the glass; partly random with respect to the food, resulting in the fish swimming away to various parts of the tank. These two phases alternated continuously; the attraction of the food always returned when it had been lost temporarily. But it was only the first 7 trials that were characterized by this behaviour. After that the fish

* Includes one "bad" performance of 2′ 27″.

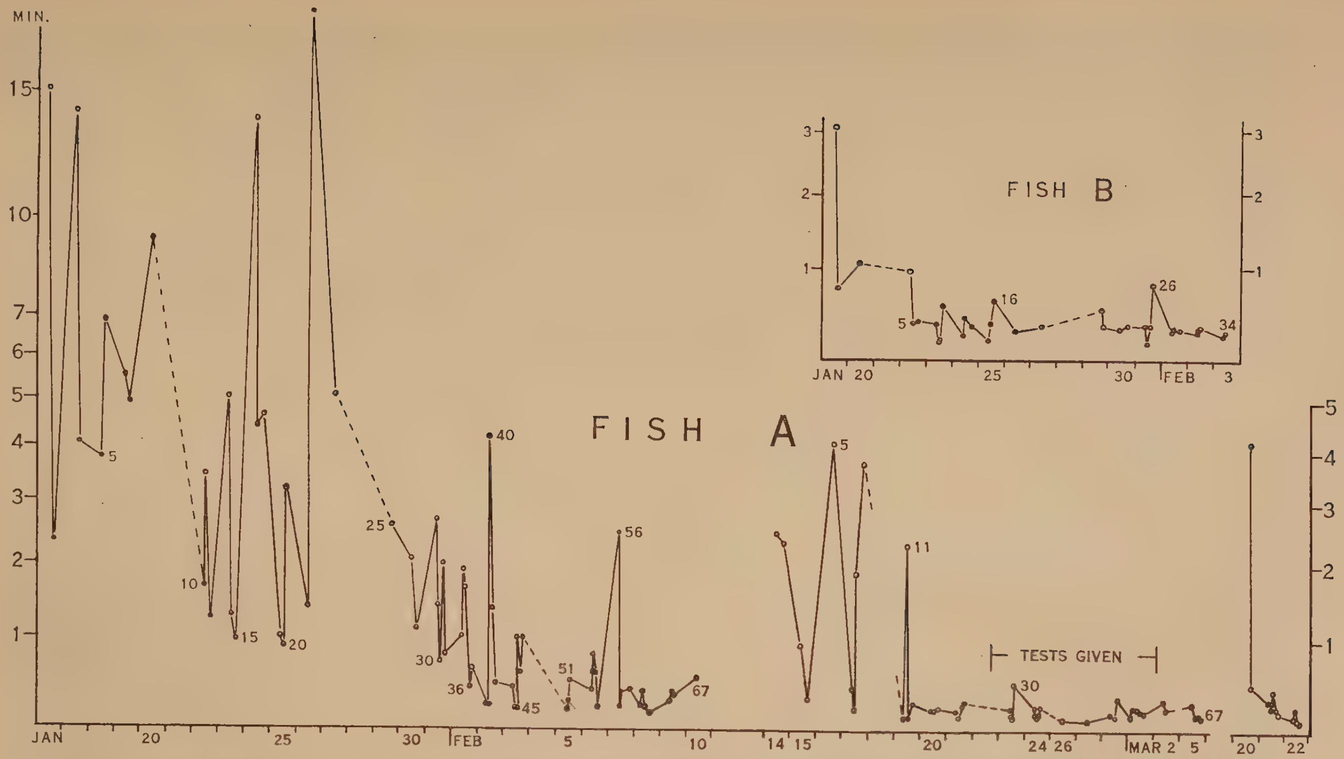

Fig. 5.—Learning graphs of fishes A and B. The duration of each normal trial feeding is plotted on a logarithmic time scale, and lines drawn between successive points. The line is broken when an interval includes one whole day on which no feedings were given. Serial numbers of the trials are placed at intervals along the graph.

was, on the whole, remarkably persistent in attacking the glass, even though the trial lasted several minutes. This was the first noticeable change in the fish's behaviour.

Another 18 trials passed without any further indication of improvement in efficiency. The average duration still showed no sign of decreasing. Trial *23* lasted over 19 minutes, during which time the fish gave no signs of having acquired anything, except the loss of the tendency to swim right away to other parts of the tank. It is all the more remarkable, therefore, that shortly after this a definite improvement became apparent. The curve (Fig. 5) shows a decided fall in its mean level at the point marked by trials *25* and *26*.

Analysis of the results shows that at this point two changes in the behaviour occurred simultaneously which together made for a marked improvement in efficiency. (1) At this point there was the first real drop in the time spent at the start of the trial in attempting to reach the food directly. Previously these times had fluctuated a good deal and were sometimes very long. For trials *19* to *23* they still maintained the high average of 2′ 20″; but in the period *24* to *29* they had dropped to 1′ 05″. (2) At this point the fish for the first time displayed a tendency to bear steadily leftwards down the glass, and this tendency was maintained.

The next " improvement " came at *36*. The fish from this point onwards firstly, often moved straight down the glass leftwards as soon as it had started moving left, and, secondly, succeeded in passing the edge *at the first attempt* four times out of five. With respect to the latter feature no further improvement was shown.

Further stages in the acquirement of a more efficient response were as follows. By *45* the leftward movement had come to be almost invariably a sideways movement along the glass, wheeling movements round the edge having become virtually eliminated (see below). At *55* the tendency to move straight down the glass as at the first leftward movement was almost established, and at this point the second marked drop occurred in the time spent in attempts to reach the food directly.

The learned response involved a swimming leftward along the glass in a more or less continuous movement until the edge was reached, the fish " feeling " its way round by making constant contact with the surface. In this movement the fish was orientated either at right angles to the glass, or, more usually, making an angle of 45°, having turned half-left. In either case the food was in the range of vision of the right eye. With regard to the process by which this response was established, one point deserves comment. During the first 25 trials, when the fish only succeeded in getting round the edge by lucky random movements, two methods of accomplishing the feat were equally frequent. Either (*a*) random working over the surface happened to bring the fish to the edge and so sometimes on and round, or (*b*) it happened to swim to the left and got round in a wide sweep. At *26*, as has been seen, there was a sudden tendency shown to work down the glass in a continuous movement ; that is to say, an efficient response began to develop out of method (*a*). Method (*a*) may be said to have started to acquire significance. But at the same time method (*b*) had been learnt in some measure, the fish sometimes turning sharply to the left and a further sharp right wheel bringing it round the edge. For a time, then, there was an antagonism between two methods. Eventually the response developed from (*a*) predominated—as in all other fish subsequently trained under the same conditions—and by *44* method (*b*) was practically eliminated. This antagonism no doubt hampered and delayed the smooth course of learning. It is possible, however, that the successful accomplishment of the trial through method (*b*) may have been partly responsible, through a " transfer of learning," for an improvement in method (*a*) shown at *36*, after which the fish normally got round at the first movement down the glass, having learnt to swim left for an appreciably long stretch.

A further complication occurred with respect to method (*a*), the movement along the surface of the glass. This was normally accomplished by the fish keeping more or less at right-angles to the glass, or turned half-left, the food being viewed through the right eye. But the first attempts in reaching the food after the first leftward movement were often made at an angle of 45° to the glass, the fish orientated *half-right* and the food in the field of *both eyes*. A certain antagonism between these two positions had therefore to be overcome. This was more clearly shown in fish B (p. 519).

In view of these complications, it is not surprising that the process of learning was long and not by any means straightforward. The action was learnt in a precarious way. Nevertheless the results obtained from other fish show that an efficient performance can be established before there is any stabilization of the actual movements performed or in the orientation adopted, and demonstrate that variation in the methods of making the detour *need* not set up antagonisms which impair the acquisition of a learned response.

Second series (trials *B1* to *67*). After an interval of four days, during which the fish was subjected to disturbance, trials were renewed. The fish proved to have lost a good deal of ground, but it was not long before it regained the efficiency acquired during the first series of trials.

The tendency to move leftwards was retained from previous training, but at first the fish was inclined to travel only for a short distance down the glass. A change came at *5*, from which trial onwards it always carried on so as at least to come close to the left-hand edge. A further rather sudden change came at *10*, after which the fish only rarely failed to pass round the edge in its first leftward movement. After *10* there is only very slight general improvement in the action of moving leftwards.

Another retention from previous training relates to the time spent at the glass opposite the food before the first leftward movement. This period was short from the start of the second series, but there was a sudden and quite marked improvement after *9*. The average duration from trials *5* to *9* was 11″, while for subsequent groups of 5 trials the values were as follows: 7″, 6″, 7″, 5″, 5″, 5″, 4″, 3″. The change at *10* coincided with the improvement noted above with respect to the continuity of the leftward movement.

When the learned response had been thoroughly established, some experiments were made to test the extent of organization of the action. The experimental conditions were modified in certain respects, and the effect on the fish's behaviour observed. These "tests" are described below.

Third series (trials *C1* to *11*). After an interval of 15 days from the completion of the second series, trials were renewed on March 20 to 22. The first took over 4 minutes; but after this trial the fish rapidly improved. Trials *2* to *6* averaged 0′ 21″, and *7* to *11* averaged 0′ 10″.

Tests in which sight of food was interrupted. In trials *B35* and *36* a prism was placed against the back of the glass, near the edge, in such a manner that, as the fish passed leftwards, the sight of the food was cut off without the intervention of an obvious partition. In the first trial the fish hesitated twice at the edge of the prism, but went round successfully the third time. In the second trial it went straight round first time. Thus it appeared that, for perfect performance of the detour response, the food need not be visible all the time.

In trial *38* a piece of mirror was placed at right angles to the glass, again cutting off the view of the food, and, instead, presenting the fish with a reflection of itself. The fish solved the trial perfectly successfully at first leftward movement. Similarly when the test was repeated (*39*). In the next trial, however, it stopped in front of the mirror and behaved as if its reflection had been detected. Trial *41* was once more performed efficiently; and trial *42*, by contrast, resembled *40*, the fish reacting energetically to its reflection.

These few trials showed definitely (1) that the fish was sensitive to its mirror reflection, and may be induced to react to it. But (2) in spite of this fact, the learned action may proceed normally, as in *38*, *39*, and *41*, although the vision of the food object is replaced by the mirror reflection. The impetus of the learned action is evidently strong enough to overcome the attraction of the mirror reflection. These tests, then, serve to show that it is not merely inessential that the food be in sight all the time, but the action has strong enough impetus to progress in spite of distractions.

Tests in which the detour was extended. In these tests the fish had to pass two partitions instead of one. It was started from K, instead of from L. The results are given below. In all eight trials the fish reached the food by working to the left. It thus passed first from K to L, and then had to perform the normal course to which it had been trained, from L round to the food.

Average of previous 9 normal trials (L to food): $10\frac{1}{2}$ secs.

Trial No.	K to L.	L to food.	Total duration (secs.).
45	8	14	22
46	92	28	120
47	264	15	279
51	12	8	20
52	11	10	21
54	8	11	19
60	16	7	23
*61**	(24)	(12)	(24)

It will be noted that the fish gave an excellent performance on the very first test, and with the outstanding exceptions of the second and third tests, showed that the conditions presented no special difficulty. The passage from K to L was made in the same manner as the learned response from L to food, and was performed as rapidly. The lapse in trials *46* and *47* involved a temporary inability to pass from K to L, and it is interesting to note that just previously the fish had been given a long unsuccessful trial from J, following which a temporary instability in its response appears to have resulted. It is, however, the efficient performance of six out of eight tests that is significant, and serves to show how a learned detour response can serve to facilitate greatly the response to a detour of greater complexity.

These tests gave a hint that the fish had acquired a tendency to move to the left rather than towards the right when meeting an obstruction, for when at K it worked toward Q rather than P. Two tests in which the fish was started from J gave further evidence of this. From this position it could reach the food either by passing one partition to the right, or three partitions to the left. One of these tests (*45a*) was unsuccessful. The fish did not reach the edge O at all, and the trial was eventually abandoned. The other (*61*) was performed successfully in 2′ 31″, the fish *working round to the left*, and eventually reaching the food by the most roundabout route. The fish had evidently acquired such a strong tendency to move leftwards that it was unable readily to adapt its movements to conditions representing the mirror image of those to which it had been trained.

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* Part of longer trial.

Fish B.

Length 7 cm.

Jan. 2, placed in experimental dish in an empty tank in the main laboratory, under conditions referred to on page 502. For a fortnight fed with Mytilus and pieces of Polychaete worm off the end of a wire, until it had become thoroughly habituated to this method of feeding. It took food somewhat more readily than fish A, which was investigated at the same time.

Jan. 17–18, first trials with the glass partitions, which however proved unsuccessful, the fish showing increasing "panic" on repeated contacts with the glass.

Jan. 19–Feb. 8, 48 experimental feedings.

Trained to plain glass obstruction, with short detour of 4·1 cm. Later transferred to detour of 6·5 cm., as presented to most of the other fish.

The fish proved more energetic than A, and at first was much disturbed on making contact with glass partitions. It was trained to a very simple detour. A plate of 8·3 cm. width was interposed between it and the food, the course on either side of it being left free. It had thus to pass sideways 4·1 cm. either to the right or the left.

The learning curve is given in Fig. 5. The averages of groups of five successive trials are as follows :

Serial No. of trials.	Average duration.	*Serial No. of trials.*	Average duration.
1–5	1′ 15″	*21–25*	0′ 18″
6–10	0′ 20″	*26–30*	0′ 25″
11–15	0′ 19″	*31–34*	0′ 15″
16–20	0′ 25″		

After only 5 trials a level of efficiency was reached, and no further improvement was shown. A constant method of solving the trial was adopted. The fish first spent a little time in attempting to reach the food directly. It then began to bear to the right, all the time keeping orientated towards the food. It continued steady rightward movement until reaching the right-hand edge of the glass, passing which it swam straight forward to the food. Except for one of the earliest trials, it always made the short detour in this manner. The variations in the durations of the trials were largely due to variation in the time spent before bearing to the right. Once it had started sideways movement it almost invariably continued until the edge was reached.

The constancy of the level of efficiency after trial *4* is noteworthy. Though there was room for improvement, none was shown after this trial.

After 34 trials, the fish was given a longer detour, of the same type as that to which other fish were trained from the start. The only difference lay in the fact that it had to move round by the right instead of the left. (Food presented at K, fish started from near corner D.) After 14 trials had been given the fish began to grow lethargic and training had to be discontinued. Nevertheless some significant results were obtained.

The average duration of groups of successive 5 trials was as follows :

1–5	0′ 46″
6–10	0′ 36″
11–15	0′ 52″

The effect of the previous training was at once apparent. No random movements were made from the glass ; there was strong tendency to move down the glass to the right, the fish keeping orientated towards the food ; and the first three trials were performed by the method previously learned. At the same time, however, the fish showed some hesitation in moving continuously down the increased length of glass. There seemed to be a limit to the distance it would readily withdraw from the food. This hesitation did not decrease : rather it led to new reactions which upset the stability of the response.

From the fourth trial onwards it began to make turns towards the right, and to work down the glass at different angles. In some trials it reverted to the original behaviour, but these were rather less efficiently performed than others. Probably on account of a certain confusion in behaviour thus introduced, the duration of the trials, after first declining somewhat, became distinctly longer than when the fish was first presented with the 6·5 cm. detour.

Fish D2.

Length : 5½ cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 11, seven feedings given. Oct. 12, frame with glass plates tested in the tank ; fish took food readily just after in spite of the disturbance. Oct. 13–Nov. 13, 45 experimental feedings.

Plain glass obstruction ; detour of 6·5 cm.

The curve for the duration of trials is shown in Fig. 6. The average duration for successive groups of five trials is as follows :

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	2′ 18″	*26–30*	1′ 14″
6–10	2′ 19″	*31–35*	1′ 0″
11–15	6′ 36″	*36–40*	2′ 51″
16–20	3′ 44″	*41–45*	2′ 30″
21–25	2′ 22″		

The experiments on this fish were abandoned, when, after 45 trials, it seemed farther off establishing a learned response than at the start.

This fish was decidedly "nervous" in the early stages, and tended to give shock reactions to the glass partitions in a manner not observed in other individuals. For some time it was only possible to give one trial a day. This effect, however, had worn off by trial *10*, and the fish's behaviour was thence normal.

For the first few trials the fish showed a strong tendency to move to other parts of the dish, though it repeatedly returned towards the food. From trial *4* onwards, however, this tendency was only shown in a modified form or appeared only after the trial had lasted a considerable time. From this point the fish worked steadily, often actively at the glass, and was unusually persistent in its attacks on it.

With regard to the failure to establish an efficient response, certain features are worthy of notice. The earlier trials were mostly solved by the fish giving a left-turn, swimming left, and right-wheeling round the edge. The left-turn movement was thus apt to lead directly to a solution. During trials *3* to *12*, 10 such left-turn moves were made, and no less than 6 were effective in this way. Yet this movement suddenly dropped out at this point. The same thing happened in the case of other fish which did eventually acquire an efficient response and is commented on at a later stage.

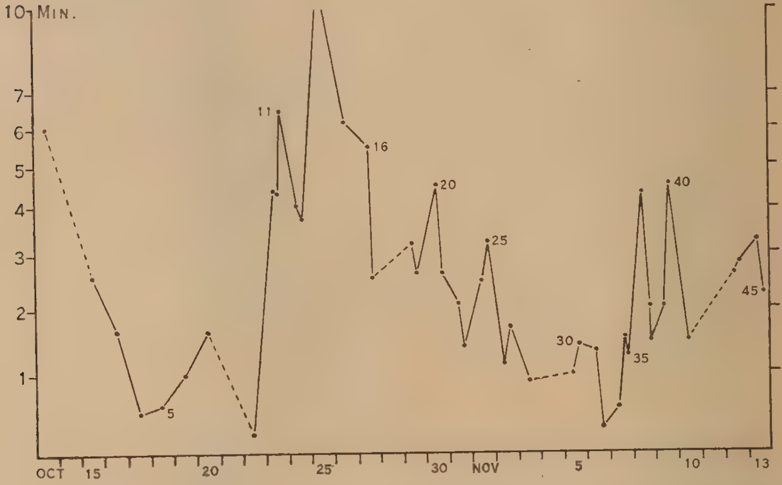

FIG. 6.—Graph of duration of trials of fish D2. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

For a period, between trials *25* and *35*, some improved efficiency was shown. Though, in the main, there was gradual improvement from *14* onwards, trials *17* and *26* mark two stages in which there was comparatively sudden change. The first point marks the complete disappearance of all random movements away from the glass, and at the same time the frequency of leftward movements along the glass (after the first) increased. The second marks quite a sudden permanent reduction in time spent in attempts to reach the food directly, another sudden increase in frequency of leftward movements, and withdrawing movements from the glass (which had been a conspicuous feature of some earlier trials) quite suddenly disappeared.

The improvement was not maintained and a marked " lapse " occurred after *35*. The trials now show an increase in time spent in attempts to reach food directly, before any leftward movement, a decrease both in *frequency* of leftward movements (after the first) and in their *efficiency*. There was also a return of withdrawing movements from the glass. It is interesting to note that the decrease in efficiency of leftward movements set in while their frequency was still increasing (trial *29*); the lapse was thus to some extent forecast.

The performances during the last 10 trials, though comparable in duration with those of the earlier, differ in some other respects. Notably, there was no return to making random movements away from the glass, or to making left-turns. If the fish had " learnt " nothing else, it had acquired the habit of working persistently at the glass. Its responses to the situation, though relatively ineffective, had become more stabilized

Fish D3.

Length: 5½ cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 12, seven feedings given. Oct. 13–Dec. 13, 83 experimental feedings.

Trained to plain glass obstruction; detour of 6·5 cm.

The curve for the duration of trials is given in Fig. 7. It will be seen that after trial *10* the curve sinks to a low level from which it sharply rises at intervals, representing intermittent inefficient performances. After *42*, inefficient performances become more frequent, until at *51* a bad spell sets in during which the durations of the trials are even greater than at the start of the experiment. Towards the end efficiency is increasing considerably, and the fish is well on the way to establishing an effective response when the trials are eventually abandoned.

From *16* to *42* there was a spell over which the times averaged 12″, if three intermittent " bad " trials, which stand out in marked contrast to the others, be omitted. During this period, then, the fish had produced an efficient response, on which, however, it appears to have had a precarious hold. The explanation of this, as well as some understanding of the bad lapse that set in, is forthcoming when the observations on the fish's behaviour are examined.

A peculiarity of the behaviour was the exceptional activity shown at the start of the trial. The fish set at the glass with a burst of energy, which, however, waned after half a minute or so. Unless it had passed the edge in this opening period of activity, the fish settled down to steadier, but still persistent, attempts to reach the food through the glass.

FIG. 7.

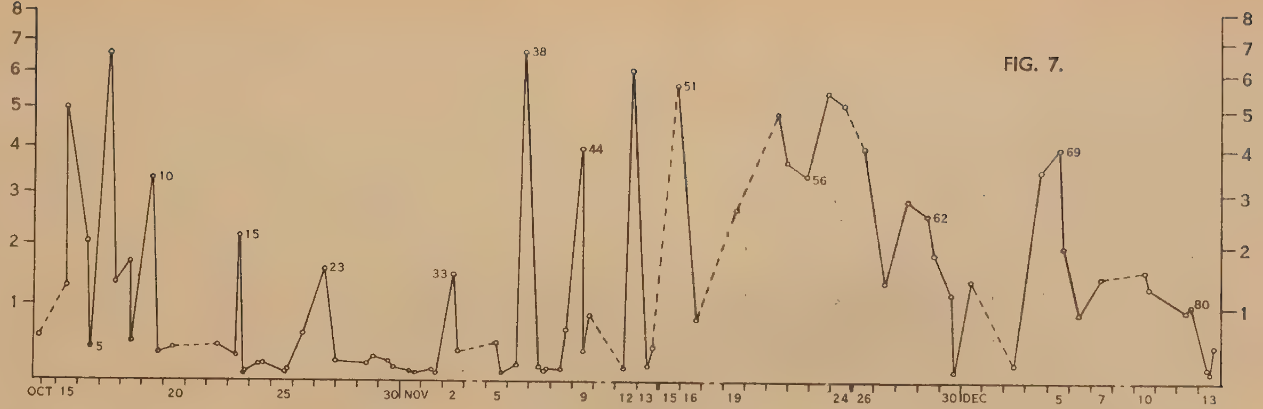

FIG. 8.

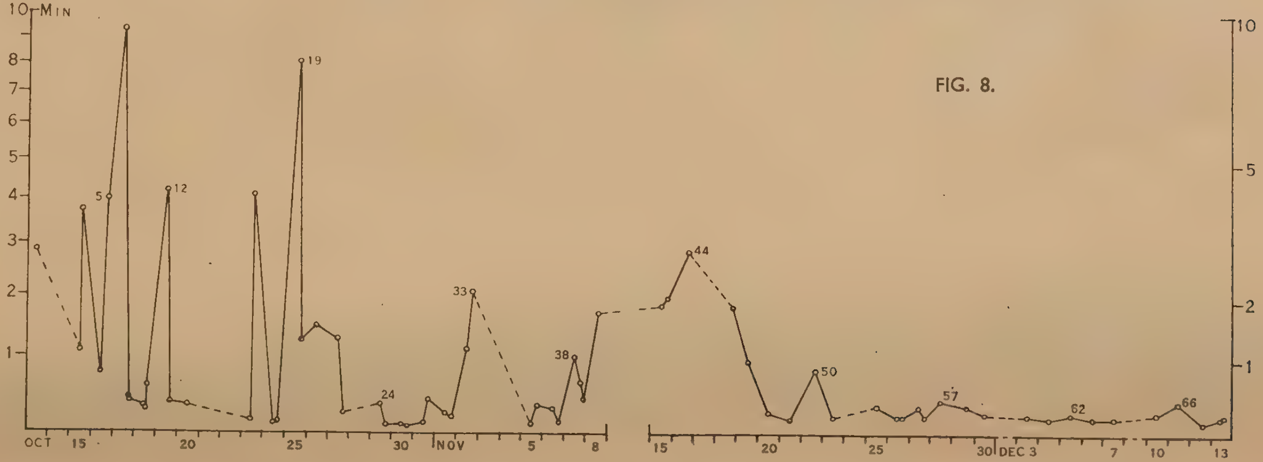

FIG. 7 (above).—Graph of duration of trials of fish D3. FIG. 8 (below).—Graph of duration of trials of fish D4. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

Another peculiarity was that the fish never made random movements away from the glass to other parts of the tank. It held persistently to its attempts at passing the glass obstruction. During the opening period of activity it was, from the start, inclined to work leftwards along the glass keeping orientated towards the food (as with fish B, p. 518). When less active it was less inclined to bear leftwards. The success of the trial, therefore, depended a good deal on the success of the efforts of the first half-minute. Several of the fish in early trials spent some time in attempting to pass straight to the food before bearing to one side. In the case of D3 the duration of this period was at a minimum level as early as the 4th trial.

The features of the behaviour shown in early trials might well have been expected to work together towards a rapid acquisition of an efficient response. And to a large extent this proved to be so. The one drawback, which was never adequately overcome, was the decrease in activity after the first half-minute. If the trial lasted beyond this period it was likely to be prolonged considerably. The conspicuous intermittent " bad " performances were due to this cause.

Compared with that of other fish, the behaviour was remarkably uniform and invariable. Also there was a decided indication of a cycle of responses repeated in each trial, if prolonged. The more energetic opening " attacks " on the glass at the start led the fish to bear left in a very short time and to bear left far enough to get near or reach the edge round which it had to pass. Working up and down the glass it was liable frequently to reach the edge during the opening period. All the time the fish kept approximately orientated in the direction of the food. As activity decreased the extent of glass traversed also decreased, and the fish settled to a quieter " attack " on the glass in the middle region of the plate. The occasions on which it came as far left as the edge R now became less frequent, and the chances of achieving a solution decreased considerably. It was not, as a rule, until the trial had lasted some while that any other movements were given. These consisted in sharp turns either to the right or the left. It is noteworthy that all the first 6 trials were solved as a result of a complete or partial left-turn. But the success of the left-turn movement, as in the case of other fish, did not lead to the establishing of this method of solution. After trial *6* the left-turns were almost entirely of a partial kind, and they soon became merged in the general leftward movement along the glass. As to right-turns, the fish had a spell of these in trials *3* and *6*, but only very occasionally in other trials.

The short durations of *9*, *11–14*, and *16* onwards were the result of the edge being passed during the more active spell. The fish, however, took some time to acquire the habit of reaching the edge, and passing it, in one continuous movement.

The bad lapse which set in between *40* and *50* was associated with an entirely new feature which appeared for the first time in *48*. In that trial the fish began repeatedly to withdraw straight back from the glass. This movement was quite a "useless" one and tended to check leftward movement. It figured largely in trial *51* and from *53* onwards, when it was regularly given after the first half- or three-quarter minute. In *54*, for example, the fish spent over 4 minutes continuously moving backwards and forwards in the middle region of the glass without once getting near the edge.

It might at first sight be supposed that the development of this useless habit was responsible for the lapse. But it is probably more true to say that it developed as *a result* of the lapse, being a symptom rather than a cause. Trial *44* can be said to mark the beginning of the lapse: the fish took 4 minutes to reach the food, but during the time did not give the withdrawal movement at all. The inefficiency of the performance resided in the fact that the fish showed disinclination to move leftwards, and, when it did so, to move far enough.

The improvement towards the end of the series was marked by a reduction in the time spent in making withdrawal movements, and the increased tendency to make half-left turns towards the edge R. Most of the later trials were solved by the latter movement.

Four tests were given with the squared glass substituted for the plain glass (see p. 561).

Fish D4.

Length: 4 cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 12, seven feedings given, food taken with exceptional eagerness. Oct. 13–Dec. 13, 69 experimental feedings.

Trained to plain glass obstruction; detour of 6·5 cm.

The curve for the duration of trials is given in Fig. 8. The averages for successive groups of five trials are as follows:

Serial No.	Average duration.
1–5	2′ 35″
6–10	2′ 07″
11–15	1′ 08″
16–20	2′ 44″
21–25	0′ 42″
26–30	0′ 11″
31–35	0′ 46″
36–40	0′ 29″
(Interval)	
42–45	1′ 53″
*47–52**	0′ 22″
53–57	0′ 17″
58–62	0′ 15″
63–67	0′ 15″

In spite of the fact that several good performances were given during the first 20 trials, and that trials *25* to *28* were performed exceptionally well, it was a considerable time before a consistent response was established.

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* Trial *48*, on consideration, omitted. Fish sluggish, behaviour abnormal.

The fish worked at the glass energetically, and was apt to make sudden darts. Its movements were rather variable. In early trials it sometimes turned left and swam into the region of corner D, and on five occasions reached the food by swimming up from this corner. It also showed a tendency to make right turns, which sometimes took it into the region of corner C, and in four trials it moved from there into K.

The movements which took the fish round the edge R to the food varied considerably. Sometimes the fish kept orientated towards the food, withdrawing along the glass surface obliquely leftward; sometimes it turned partially to the left, keeping the food within range of vision of its right eye; sometimes it turned left and wheeled round the edge. And there were modifications of these three main methods. It is noteworthy that, after *12*, the third movement proved an effective method of solving the problem. Yet for a long time it was only occasionally attempted.

In spite of the variable quality of its reactions to the obstruction, the fish, after *23*, gave a series of performances in which its methods were consistent (the first of those enumerated above). At first, too, it seemed to have established a consistently *efficient* response, but lapses set in. By Nov. 7–8 the fish appeared definitely to be in sub-normal health, and after *41*, the series of experimental feedings was interrupted. Trials were suspended until Nov. 15, during which period the fish was fed normally in an ordinary manner, off the wire.

When trials were resumed (*42*) the fish had recovered normal activity. Trials *42* and *43* were solved in just under two minutes, both by the third method. The fish, then, had lost the previously established tendency to make the detour by method 1. But, at the same time, it had retained certain features from its previous training. (i) It had come to move leftwards almost immediately, never spending more than 8 seconds in attacking the glass in the original position; and (ii) it had come to keep up a persistent attack on the glass not making any movements away to other parts of the tank.

As indicated by the figures for the duration of the trials, a sudden change came at *47*, which marked the beginning of a series of efficient performances. A learned response can now be said to have been established: the sudden improvement is noteworthy. It is also of interest to note that the variable quality of the fish's responses, which had reappeared after *43*, persisted for some time after efficiency was established. The method of solution was not stabilized until efficiency had been attained. The significance of this feature is discussed on page 551. Towards the end the left-turn-and-right-wheel movement tended to predominate.

Fish D5.

Length : 5 cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 13, eight feedings given. Oct. 15–Dec. 13, 102 experimental feedings.

Trained to plain glass obstruction ; detour of 6·5 cm.

The curve for the duration of trials is given in Fig. 9. The averages for successive groups of five trials during training are as follows :

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	11′ 36″	*21–25*	0′ 36″
6–10	5′ 51″	*26–30*	0′ 13″
11–15	3′ 18″	*31–35*	0′ 14″
16–20	0′ 48″	*36–39*	0′ 12″

Before the 40th trial an efficient learned response was securely established, and after this various tests were performed on the fish. In spite of apparently hopeless efforts in early trials, this fish emerged as the most proficient performer of those trained to the plain glass obstruction.

The earlier performances were outstandingly " bad." The fish was excessively disposed to wander over various parts of the tank, particularly in the right-hand part, and only eventually reached the food when it happened to move round near it. After twelve trials had been given it seemed no nearer a learned solution of the detour than at the start, and appeared to be a hopeless case. Yet by the 18th trial it was well on its way to acquiring an efficient response, which was established from *24* onwards. An improvement came with comparative suddenness, following on a remarkable change in the fish's behaviour. The change may be said to have dated from the end of *13*.

The manner of the fish in early trials contrasted sharply with that of fish D4. Its movements were characteristically leisurely and it was not subject to more violent bursts of activity. In contrast with fish D1 (p. 531), however, it had little tendency to persist in working against the obstruction, but constantly reacted by turning and swimming away from the glass to some other part of the tank. However frequently it might return in the direction of the food, this lack of persistence remained. The solutions of the early trials were more conspicuously fortuitous than in the case of any other fish. Of the first twelve, five involved swimming up from corner D, in three the fish swam in an arc between R and D from the front of the tank, and in three an approach was made from corner A. Only in two (*5* and *9*) did the fish keep at all close to the glass in moving leftwards round the obstruction, in both of them turning left and wheeling round to the right. No habit was developing which could provide a basis for a learned response.

Trial *13* progressed on the same lines as the previous inefficient trials. The fish had had three short spells at the glass, when random movements brought it into the right side, and thence to the back part of the tank. It moved round again to corner C, and, 2′ 15″ from the start of the trial, moved up to the food in the original position. It then behaved in a changed manner: it bore leftwards, keeping close to the glass, continued till the edge was reached, and passed the edge at 2′ 25″, snapping at the food immediately after. It had never made the detour in this manner before.

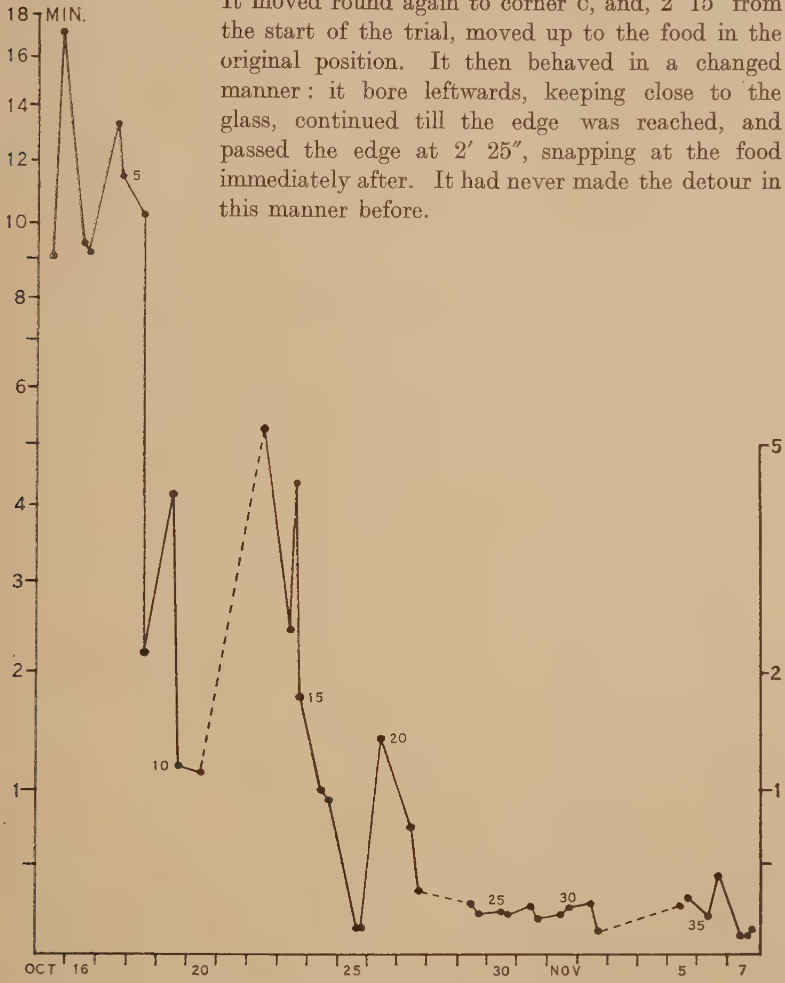


FIG. 9.—Graph of duration of trials of fish D5 during training. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

The type of behaviour shown at the end of *13* persisted in all subsequent trials. Though *14* was not solved until over 4 minutes, the whole of the period was occupied with leftward movements along the glass. Though the fish had still to learn to work more continuously leftwards and to desist from minor withdrawing movements, the contrast between this performance and preceding trials was most striking. And the changed behaviour was permanent. Persistent working over the middle and leftward side of the glass almost completely replaced other movements. The reaction of turning sharply to right or left and swimming away from the glass suddenly and completely dropped out. The data given in Table II illustrate this feature. Moreover, turning movements of any sort were only very rarely given. Only two full left-turns were noted in the whole series of trials from *14* to *39*, and no right-turns at all. Even half-left turns were only very occasional.

TABLE II.

FISH D5: RANDOM MOVEMENTS AWAY FROM OBSTRUCTION.

Trial.	Period spent at glass.	Turns L. toward corner D.	Turns L. toward front of tank.	Turns R. toward corner C.	Remarks.
5	1′ 47″	1	–	4	
6	8′ 10″	1	7	7	
7	c. 7′ 00″	7	7	4	
8	2′ 05″	3	4	2	
9	4′ 05″	3	4	3	
10	0′ 30″	–	–	2	
11	1′ 05″	1	3	–	One withdrawal.
12	c. 4′ 00″	2	5	3	
13 (first period)	0′ 42″	–	2	1	
13 (second period)	0′ 10″	–	–	–	
14	4′ 20″	–	–	–	Several withdrawals.
15	1′ 44″	–	–	–	,, ,,
16	0′ 58″	–	–	–	
17 onwards	–	–	–	–	No withdrawals after *21*.

The method of solving the trial achieved for the first time at the end of *13*, by working leftwards close to the obstruction and finding the way round the edge R, characterized all subsequent trials. It has to be noted, however, that the actual movements which took the fish round the edge still varied considerably, and continued to vary after efficiency in performance had been acquired.

After the change of behaviour, it was not long before a marked improvement in the efficiency of the fish's performance became noticeable. Trials *18* and *19* both were solved in less than 10 seconds. After *21*, trials were consistently good. The steady improvement is indicated by the figures given in Table III. It will be noted that leftward movements increased both in frequency and in efficiency.

TABLE III.

Improvement in Performance of Fish D5.

Trial *Serial No.*	Total duration.	Leftward movements per min. (i) Total per min.	(ii) Unsuccessful.	(iii) Successful.	Ratio unsuccessful : successful—(ii) over (iii).
14	4′ 21″	1·6	1·4	0·2	6
15 to *20*	5′ 13″	3·3	2·1	1·1	1·8
21 to *39*	4′ 18″	7·2	2·8	4·4	0·6
Period of Maximum efficiency. Normal trials, between *80* and *101*	1′ 36″	11	2	9	0·2

Tests.

Food presented on the right. From *40* onwards certain tests were performed on the fish which were intended to throw light on the nature of the learned response. One series of ten, carried out at regular intervals between *40* and *58*, consisted in presenting the fish with, so to speak, a mirror-image of the conditions to which it had been trained. The food was presented at K, and the fish had to move to the right round edge Q. The results are summarised in Table IV.

TABLE IV.

Fish D5: Tests in which Food was presented on the Right of the Dish.

Test *Serial No.*	*Trial* *Serial No.*	Duration Test.	Normal trial.	Remarks.
A 1	*40, 41*	13′ 00″+	0′ 10″	
2	*42, 43*	0′ 26″	[2′ 43″]	
3	*44, 45*	0′ 22″	0′ 28″	
4	*46*	0′ 10″	0′ 12″	
5	*47, 48*	1′ 02″		
6	*49, 50*	0′ 31″	1′ 02″	
7	*51, 52*	1′ 53″	1′ 36″	Very marked tendency to withdraw appears.
8	*53, 54*	10′ 00″+	0′ 17″	
9	*55, 56*	14′ 00″+	2′ 25″	Again marked tendency to withdraw.
10	*57, 58*	4′ 15″	0′ 25″	,, ,, ,, ,,

The times marked with a plus sign indicate that the trial was abandoned before the fish reached the food.

In all cases the test trial was given first, followed by a normal one. An unfortunate result of the tests was that the normal performances were somewhat upset, one conspicuous bad habit developed in the former—that of withdrawing repeatedly from the glass—being transferred to the latter.

Nevertheless one or two definite points emerge. In the first place, the performances of the tests are seen to fall sharply into groups. (1) The fish proved quite incapable of giving adequate rightward movements, and the behaviour in the tests differed conspicuously from that in the normal control: these tests include *1*, *8*, *9*, and *10*. (2) There was no significant difference in the performance on the two sides, and the learned behaviour can be said to be completely transferred: viz. trials *2* to *7*. The fish thus exhibited two quite distinct behaviour patterns under the new conditions.

Secondly, the fact that the fish was capable of exhibiting transfer of learning without having to learn the new detour anew is worthy of notice. Tests *2*, *3*, and *4* were all performed as efficiently as could have been expected were transfer of learning a reality. Also it may be noted that the first test was all but solved in an extremely short time, the fish just failing to pass the edge at 5″ (after which it never moved to the right again).

A "bad" habit, involving the useless movement of withdrawing repeatedly from the glass for a short distance, appeared first in tests *1* and *7* and was again shown in the normal trial which followed the latter. The movement became conspicuous in trials which followed, and a series of normal trials had to be given to train it out. After *67* normal efficiency was re-established. Evidently, then, the tests set up a certain instability in the fish's behaviour.

Fish started from other parts of dish. Between *74* and *102* the tests consisted in starting the fish from some part on the right-hand side of the tank, the food placed in the normal position. The fish thus had to make a longer detour, and two courses were opened to it, either round to the right and up to food passing edge o, or round to the left. It was found that the fish sometimes took one route, and sometimes the other. The main feature shown was that the passage round to the right took, on the average, a longer time, and evidently presented greater difficulties, than that to the left. This is seen from the figures given below, derived from combining all the tests, and averaging the times spent in reaching the food from three starting-points. A large difference is seen between the rightward and leftward courses. Evidently, then, the learned response had established a facility for leftward movement.

TABLE V.

FISH D5: COMBINED RESULTS FROM TESTS IN WHICH THE DETOUR WAS EXTENDED.

The figures denote average of time taken to reach food from the positions indicated.

From position . .		BF	EB	
		2′ 22″ ——→	1′ 41″	Rightward movement.
	0′ 46″ ——→	0′ 31″ ——→	0′ 09″	Leftward movement.
From position	BF	FC	GC	

The end part of the rightward course, round the edge O, resembled a mirror-image of the normal conditions (passage from GC). It is therefore comparable to the conditions presented in the first series of tests, in which the fish had to make a passage round Q. It may be noted that the fish's behaviour in the first two trials (*73* and *79*), in which it had to find its way round O, compared with its behaviour in the former tests. On the first occasion it failed to get round O at all, showing no inclination to bear to the right. The second showed complete transfer, the performance being accomplished efficiently in 10 seconds.

The interpretation of the process of learning exhibited by the fish is further considered in the discussion (pp. 549–552).

Fish D1.

Length: 5½ cm.

Sept. 25, transferred to experimental dish; P.M., took food. Sept. 27–Oct. 11, seven feedings given; soon came to take food readily. Oct. 12, frame tested in dish; disturbance sets up fright reactions in the fish, which would not take food immediately after; but fish took food readily two minutes later. Oct. 13–19, seven feedings. Oct. 20–Dec. 7, 61 experimental feedings.

Trained to plain glass obstruction, with glass bordered on top, bottom, and at left edge with a black strip, ½ cm. wide. Detour 6·5 cm.

The curve for the duration of trials is shown in Fig. 10. The average duration for successive groups of five trials is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	1′ 07″	*26–30*	0′ 48″
6–10	3′ 33″	*31–35*	1′ 05″
11–15	4′ 19″	*36–40*	2′ 26″
16–20	0′ 55″	*41–45*	2′ 21″
21–25	2′ 28″		

The fish was characteristically a steady worker, moving slowly and deliberately. It never exhibited any marked bursts of activity. From the start it showed a tendency to work persistently at the glass, and never moved off to the right-hand side of the tank.

The only movement it made away from the glass involved a full left-turn and passage to corner D or to the front of the tank. During the earliest trials, twice did the fish swim up to the food from corner D, and on three occasions a full left-turn followed by a right-wheel took the fish round the edge R. But after the 6th trial the left-turn movement suddenly dropped out of the fish's repertoire and was only given on one other occasion during the next 36 trials.

As the above figures indicate, the fish failed to establish a learned response. There were two periods in which improvement appeared to be coming, but the promise was not fulfilled. And this in spite of the fact that the fish's behaviour was perhaps more stereotyped than in any other

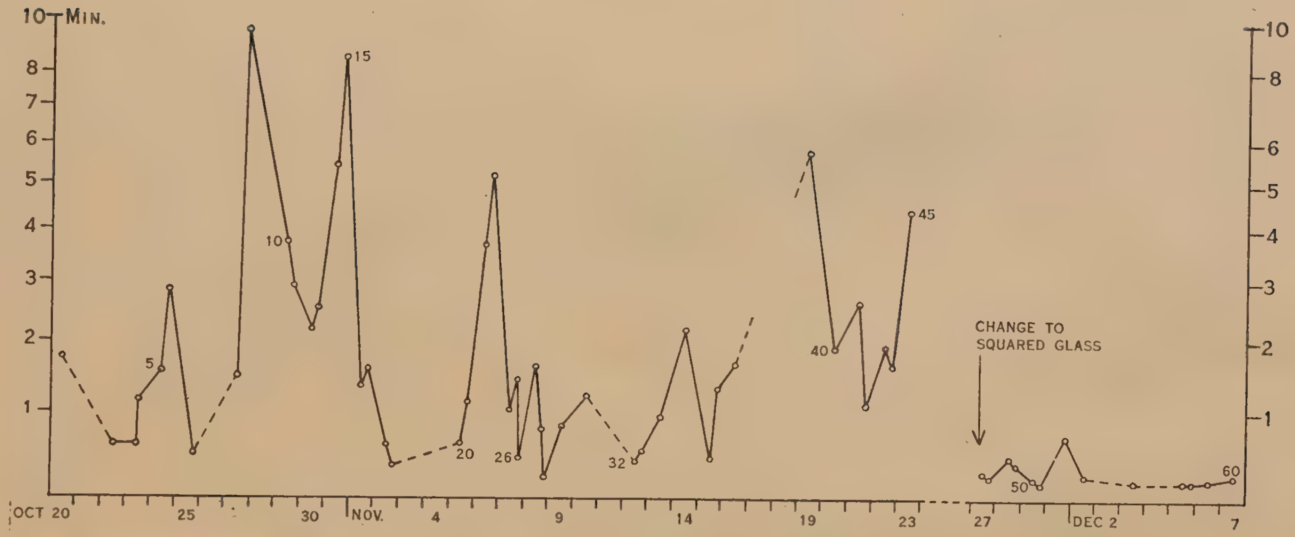


FIG. 10.—Graph of duration of trials of fish D1. Note the sudden change to an efficient performance when squared glass was substituted for plain glass (see p. 561). Two normal trials given the latter period were abandoned unfinished at 3 minutes.

fish. With the exception of the left-turn movements mentioned above, it kept remarkably uniform throughout. The fish settled into a habit of reacting to the obstruction in a certain manner which eventually led to its passing the edge. Yet the performances did not consistently improve.

Some tests were performed on this fish in which the plain glass was replaced by another on which a meshwork of fine lines had been scratched (p. 511). The results were striking, the fish giving a series of perfect performances, showing that something had been learned during the first 45 trials. These results are dealt with on pp. 560–561.

This fish gave no evidence that the black edge of the glass had any effect in facilitating the passage round the detour. Neither were any special reactions given to the band, nor was the fish induced to perform movements different from those given by other fish against plain unbordered glass.

Fish D6.

Sept. 25, transferred to experimental dish; P.M., took food with gentle coaxing. Sept. 27–Oct. 18, 13 feedings given. Oct. 19–Dec. 13, 75 experimental feedings.

Trained to plain glass obstruction, with glass bordered on top, bottom, and at left edge with a black stripe, ½ cm. wide. Detour 6·5 cm.

The curve for the duration of trials is shown in Fig. 11. The average duration for successive groups of five trials is as follows :

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	1′ 34″	*41–45*	1′ 04″
6–10	4′ 12″	*46–50*	1′ 05″
11–15	5′ 18″	*51 55*	0′ 45″
16–20	4′ 58″	*56–60*	0′ 44″
21–25	3′ 28″	*61–65*	0′ 40″
26–30	1′ 06″	*66–70*	0′ 42″
31–35	0′ 58″	*71–75*	0′ 54″
36-40	1′ 08″		

The durations thus settle down to a uniform average level of about ¾ minute. This comparatively high value is due to the fact that the fish learned the alternative circuitous path to the food, moving to the right and passing three partitions (Fig. 1, partitions Q, P, and O). D6 was the only fish to give this curious result.

It is of special interest to examine the early behaviour to discover the steps which led to the acquisition of the response. Careful analysis of the movements made by the fish during early trials has shown certain features which can only be summarized here.

(i) From the start the fish had a tendency to react to the glass by making sharp turns to the right or left. The first four trials were solved as a result of a left turn; in two cases the fish wheeled widely round the edge, in two it swam into corner D and up to the food from that point.

FIG. 11.

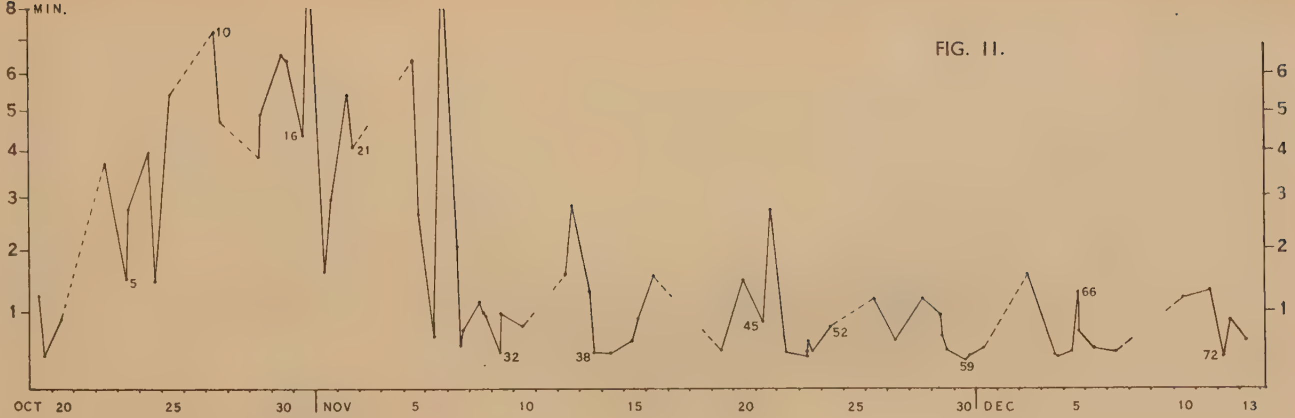


FIG. 12.

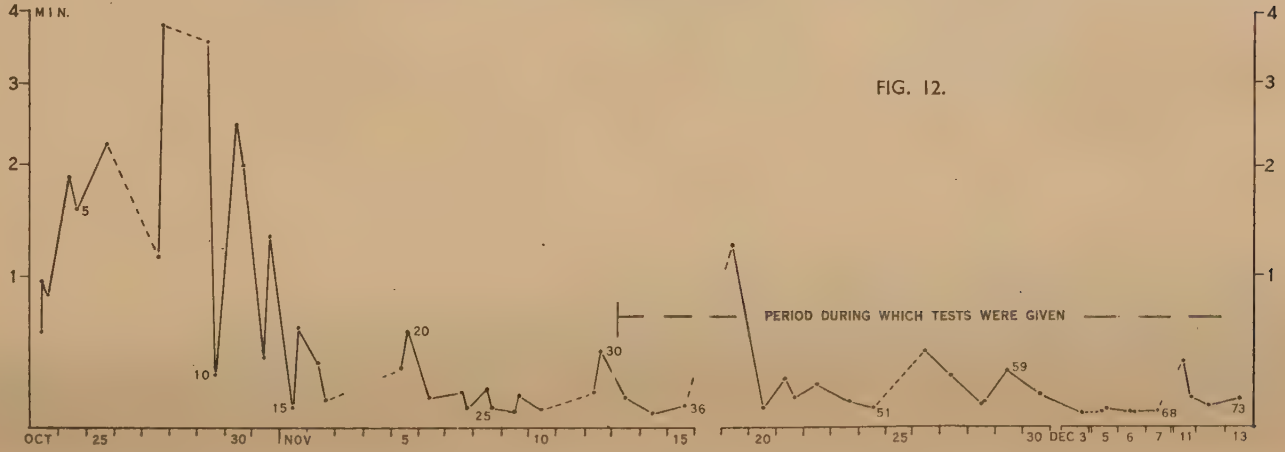


FIG. 11 (above).—Graph of duration of trials of fish D6, which acquired the habit of making the detour by the roundabout route.

FIG. 12 (below).—Graph of duration of trials of fish D7. From Nov. 13 onwards various tests were regularly given: only the normal control trials are given in the graph.

(ii) A new feature of behaviour appeared in trial *4*: the fish began repeatedly to withdraw from the glass along the line of its approach (i.e. back in the direction of corner C). This trait persisted and came to be an outstanding peculiarity of the behaviour of this fish, normally characterizing the opening period of almost all trials from *4* onwards.

(iii) Left-turn movements, occasionally given in early trials, were very successful in leading to a solution. Yet they became less and less frequent, and virtually disappeared after trial *13*. Several other fish showed this feature. Right-turn movements were more frequently given than left turns, and their frequency, if anything, increased. This feature was not shown by any other fish. It is evidently connected with the fact that the right-turn movement became associated with the withdrawing movement mentioned above.

(iv) Almost as soon as the withdrawing movement appeared, right-turn movements became associated with them. The effect was that the fish now frequently turned past edge Q into the region K. Other fish in early trials occasionally found their way into this compartment, but none so persistently as D6. From this position the fish almost always passed farther to the right, round into region J. Here it once again found only a single partition between itself and the food, and further movement to the right usually took it round the edge O. From trial *5* onwards the fish normally reached the food from this side of the tank.

(v) Finally, the fish showed exceptional disinclination to bear leftwards along the glass partition in its first assaults. This movement in fact was only given on three occasions during the first 10 trials (as contrasted with some 40 full turns). On first making contact with the glass opposite the food, the fish began withdrawing movements almost at once, and soon found its way into compartment K.

The tendency, then, to withdraw and bear right (in spite of the success of left-turns in the earliest trials) resulted in the fish working round the tank to the right and approaching the food from the direction of A. Trials *5*, *6*, *8*, *9*, *11*, and *13* were solved in this manner. Moreover, from this point onwards this course was invariably taken, and came to be followed with increasing efficiency.

It was some time, however, before any real improvement could be noticed. The time taken to reach compartment K varied from 5″ to over 4 minutes, and frequently the fish moved back round Q. Occasionally, too, it would pass back into K after reaching J. The time spent in circumventing edge O varied from 31″ to 3′ 39″. Eventually, a rather noticeable improvement came suddenly at *23*. From this trial onwards the course was followed continuously: only on one occasion (*25*) did the fish move back from region K. The passage from Q to P was now performed with very little hesitation, the time taken not exceeding 13″, and falling to an average level of 10″, gradually decreasing to 6″. The time spent in making the passage round O for a period of 20 trials did not exceed 35″, with a minimum of 9″. Efficient performances of total duration between 25″ and 40″ became increasingly frequent.*

As time went on the fish became increasingly adept at threading its way round the glass obstructions, until it was not far short of acquiring a complete co-ordinated response. It is probable that, with repetition, co-ordination of successive motor responses was occurring to some extent. Just before trial *46*, during a delay in the presentation of the food, the fish was observed to swim round the whole course in about half a minute, though there was no food present. At trial *56*, and again on the last day that experimental feedings were given, the fish swam the whole course on its own initiative in the minimum time of 25″.

Certain tests with this fish deserve notice. In the first place it was found that the black border on the glass plate SR could be removed without the least effect on the reactions of the fish. From trial *50* onwards plain glass was always used. In view of comparable evidence from fish D1 (p. 533), it may be inferred that the existence of this band does not aid the fish in perceiving the glass plate as an object.

Secondly, valuable evidence was obtained that the passage round the glass maze to the right was not dependent on influences external to the dish—for instance, such impressions of objects beyond the maze as may have figured in the fish's visual field. In trial *59* the frame was reversed, the fish started from A, and the food presented at K. The relations of the fish and food to the maze were thus unaltered, but the fish had to swim away from the light and towards the observer. The fish gave an exceptionally efficient performance, reaching the food in 22″. The same conditions were repeated next trial (*60*) and again the fish traversed the route with little hesitation, reaching the food in 25″. Further, it was found that, in normal trials, the position of the light could be varied without any effect on the fish's response. Evidently then, the fish's movements were made relative to the food and frame and were independent of features external to it.

With this fish, learning as it did a comparatively long detour, unusual opportunities were afforded for examining the learning of different parts of the route. If backward association occurred (see p. 553) it might be expected that the last part (passage round O) would be acquired first, and

* Viz.:

Serial No. of trials.	Number of efficient performances.	*Serial No. of trials.*	Number of efficient performances.
21–30	2	*51–60*	6
31–40	4	*61–70*	6
41–50	4		

the efficient performance of movement into K acquired last, only after the passage round P and O had become a fully co-ordinated movement. Analysis of the records shows no indication of any feature of this sort.

The route is conveniently divided into three sections. (1) Start of trial to passage round Q; (2) passage round Q to passage round P; (3) passage round P to passage round O. All through, the second section was more quickly and efficiently traversed than either of the others. The average times (in secs.) for successive five trials after *25* were 10, 9, 8, 6, 8, 9, 6, 6, 7, with no abnormally long times to overweight the average value. The corresponding times for the passage from P to O (3) were 64, 27, 21, 33, 27, 21, 20, 22, and 34. It appeared evident that the closer proximity of the food when the fish reached position J acted as a hindrance to the efficient passage round O. Again, though both for a time varied considerably from one trial to another, the duration of the final passage from P to O was all along somewhat greater on the average than that from the start to Q (section 1). The final section of the detour therefore presented greater difficulties than any other. And though the efficiency of performance of the different parts increased in rather too fluctuating a manner to show any definite precedence for any one, it can at least be said that the latter section was certainly not learned in advance of the rest.

Fish D7.

Oct. 10, transferred to experimental dish from another similar dish. Oct. 13–Oct. 22, 7 feedings given. Oct. 23–Dec. 13, 73 experimental feedings.

Trained to glass marked with meshwork of fine lines (p. 511). Detour 6·5 cm.

The curve for the duration of trials is shown in Fig. 12. The average duration of successive groups of 5 trials during uninterrupted training is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	1′ 10″	*16–20*	0′ 25″
6–10	2′ 13″	*21–25*	0′ 10″
11–15	1′ 17″	*26–30*	0′ 12″

This fish proved a good subject. It worked actively and persistently, was not easily distracted, and was not given to making erratic movements. It seldom made any movements away from the glass to other parts of the tank, and on the rare occasions when it did so, it soon returned to the glass.

During the first three trials the only reactions given after continued failure to reach the food direct were full turns to the right or left. Each of these trials was solved in under a minute as a result of the first full left turn.

A complete change of behaviour was shown in the next four trials, which were less successfully performed : the fish now worked close to the surface of the glass, and showed but little tendency to turn to the side. It eventually worked its way round the edge R. During these trials the first indication was obtained that the fish detected the lines on the glass, for its passage down the glass was jerky, and it appeared definitely to move from one square to another.

In the trials that followed there reappeared a tendency to give full turns, predominantly to the left. Between trials *10* and *20* a steady improvement took place, and *21* marks the onset of a spell of uniformly efficient performances.

The period of improvement was marked by an increase in both frequency and efficiency of left-turns, right-turns and other movements dropping out. The method by which the fish passed round the obstruction was constant from *9* onwards : it turned full-left, swam left, and wheeled to the right round the edge. This response became established.

There are two noteworthy features in connexion with this learned response. Firstly, the response is one which *other fish, trained to the plain glass, proved incapable of establishing*, although all performed several early trials successfully *by this manoeuvre* (see p. 548). Secondly, the fish soon came *to give the left-turn movement on its first passage up to the food before first coming in contact with the obstruction.* This never occurred in the case of fish trained to plain glass. The fish turned left regularly on reaching a point 2 to 3 cm. distant from the glass ; and this may be taken as a good indication that it detected the pattern of lines at this point. No doubt the pattern also served as a guide to the edge of the glass, and enabled the fish to wheel right at the correct moment. At any rate, the contrast between the behaviour of this fish (together with D8, p. 539) and that of other fish is a striking fact.

Tests in which food was presented at K. Between *31* and *52*, eight tests were performed in which the conditions presented a mirror-image of those to which the fish had been trained (as with D5, p. 526).

TABLE VI.

TESTS WITH FISH D7.

Food presented at K, fish started from D.			Plain glass.		
Nos. of trials.	Duration.		*Nos. of trials.*	Duration.	
	Test.	Normal.		Test.	Normal.
31, 32	0′ 26″	0′ 10″	*45, 46*	1′ 34″	0′ 15″
33, 34	0′ 25″	0′ 05″	*47, 48, 49*	0′ 09″, 0′ 18″	0′ 09″
35, 36	0′ 08″	0′ 08′	*50, 51*	1′ 31″	0′ 07″
37, 38	1′ 44″	1′ 15″	*54, 55*	0′ 20″	0′ 18″
39, 40	0′ 06″	0′ 07″	*56, 57*	0′ 34″	0′ 07″
41, 42	1′ 40″	0′ 16″	*60, 61*	0′ 09″	0′ 10″
43, 44	0′ 05″	0′ 10″	*64, 65*	0′ 24″	0′ 08″
52, 53	0′ 16″	0′ 25″	*67, 68*	0′ 21″	0′ 06″
			72, 73	0′ 18″	0′ 10″

The performances of the fish were, on the whole, essentially comparable with the normal tests performed immediately after, and indicate an almost complete "transfer of learning."

Tests in which plain glass was substituted for squared glass (Table VI). Ten of these tests were given between *45* and *72*. The durations of performances varied somewhat, but were on the average considerably higher than the normal control tests. Only two were performed as efficiently as the normal. It is evident that the fish found the conditions more difficult; yet the performances are clearly much better than if the fish had had no previous training. The level of the first five trials is somewhere about that of the 12th in the main series: there is, then, some sort of "transfer."

As regards the method of solving these tests, it is of interest to observe the difference made by the absence of the scratched lines. Whereas in the normal trials the fish now invariably turned left before reaching the glass, in the tests it always swam straight into the glass. It then spent a longer or shorter time working close up against the glass, sometimes delaying considerably before bearing leftward. Sooner or later, however, the fish would suddenly turn left and continue, wheeling round the edge. The variations in the times of the tests depended mainly on how long it took the fish to make a full left-turn.

It is of further interest to note that the method of solution of the tests with plain glass was (*a*) identical with the method learned during training to the squared glass, although (*b*) the method was never regularly adopted by the various fish trained to plain glass, evidently presenting considerable difficulties in the normal course.

Fish D8.

Sept. 25, transferred to experimental dish.
Oct. 23–Dec. 13, 77 experimental feedings.
Trained to glass with meshwork of fine lines, as was D7. Detour, 6·5 cm.

The curve depicting the duration of trials is shown in Fig. 12. The average durations of successive groups of five trials during uninterrupted training is as follows:

Serial No.	Average duration.	*Serial No.*	Average duration.
1–5	6′ 22″	*16–20*	0′ 48″
6–10	5′ 12″	*21–25*	0′ 33″
11–15	1′ 25″	*26–30*	0′ 20″

The manner of this fish differed considerably from that of D7. In early trials it was more active, and a good deal more erratic in its behaviour. More prone to make full turns away from the glass,

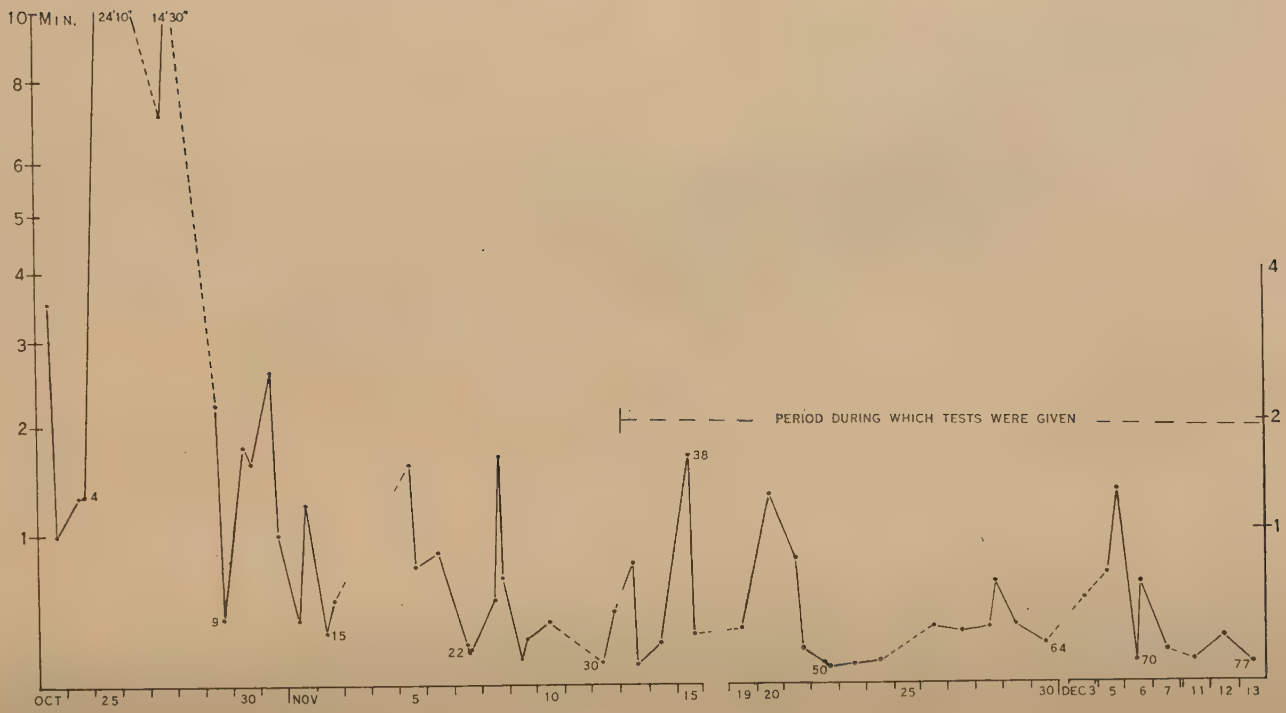


Fig. 13.—Graph of duration of trials of fish D8 as in Fig. 12.

it frequently swam off to other parts of the tank. All through it proved a more unreliable performer, and would doubtless have been long in acquiring a learned response to plain glass.

In spite, however, of this "temperamental" difference, this fish acquired a learned response of the same kind as D7, and the course of learning was in many ways similar, though less regular. The value of the results from this fish lie in the way they tend to duplicate the results from D7, and in the support they lend to inferences derived therefrom.

The solution of the first five trials was fortuitous: the fish happened to reach a part of the tank (region of corner D) from which there lay an uninterrupted path to the food. The trials which followed, however, came to be solved by a complete movement, starting with a left-turn and a right-wheel round the edge. It was this movement, which, as in D7, was established as a learned response: all solutions were effected by this means from trial *6* onwards.

As has been mentioned, the fish was much inclined to give sudden turning movements away from the glass. After giving one of these it often continued to swim right away from the glass. It became unusually inclined to wander over the tank, especially as the trial progressed. This tendency led to two excessively long trials—*5*, which holds the record of 24′ 51″, and *7*, which lasted 14′ 30″. Wandering movements, however, decreased greatly after *7*, and virtually dropped out after *12*.

Among the reactions given to the glass turning movements predominated. The fish was even less inclined to make lateral leftward movements along the glass than was D7. After *11* they virtually disappeared altogether. Withdrawing movements were rare.

A marked improvement came about at the stage of trials *11* to *13*. Before *11* no trend of improvement of performance can be observed. At this stage, however, several indications of a change occurred almost simultaneously. (1) *12* was the last trial in which the fish spent any time away from the glass; (2) after *12* turns were all to the left; (3) after *13* the time spent in attempts at reaching the food directly fell to a level minimum; (4) frequency of left-turns showed two sudden increases, one between *11* and *12*, the other between *13* and *14*; (5) behaviour became standardized from *12* onwards—leftward movements were now definite left-turns.

The subsequent progress was more gradual than in D7, and the fish continued to give occasional lapses. When, at *31*, tests were started, the fish had not acquired the same uniform level of efficiency as had D7 by this time. The acquisition of the same learned response was, however, well on its way, and the fish was beginning to turn left immediately, before touching the glass.

Tests in which food was presented on the right. Between *32* and *56* a similar set of tests were performed as on D7. Probably because the learned response had not been adequately established, this fish did not show such complete " transfer of learning " as D7. Also, the times of the " normal " tests were rather too erratic to justify close comparisons of the tests and their controls. Nevertheless, one feature may be pointed out. The first test showed the fish wellnigh incapable of adapting itself to the changed conditions. It worked persistently at the glass attempting to reach the food directly. It frequently turned to the left, but showed no tendency to turn right. Eventually, after 6 minutes, it reached the food by sheer accident. The next four tests, however, were performed differently, and the performances much resembled those of the corresponding normal trials, showing good " transfer." Though still showing some inclination to turn left, and still spending a longer time before bearing to the right, the fish solved the tests adequately by turning right and left-wheeling round the edge. In *6* and *10* the test was inefficiently performed, but *7*, *8*, *9*, and *11* were done in short times, only slightly worse than the control.

The contrast between test *1* and the four which followed is reminiscent of a similar contrast shown by fish D5, on which comment has already been made (p. 529).

As far as the extent of " transfer " is concerned, if allowances are made for its less reliable behaviour, D8 tends to bear out the features shown by D7.

Tests in which plain glass was substituted for the squared. The fish reacted in a similar manner as D7, but found the test considerably more difficult. Nevertheless, as in D7, it made the detour more readily than if no previous training had occurred ; and, again as in D7, the mean of the first five tests fell at the same level as represented by trial *12* in the main series. Other results agree closely with those given above for the other fish. The fish never turned left before striking the glass ; the solution was reached by the same method as that to which the fish had been trained ; and the variations in the times were mainly dependent on how long it took the fish to turn left.

III. Summary of the Performances of Individual Fish.

DETOUR OF 6·5 CM.

Plain glass obstruction.

Fish A. *Efficient learned response*, after 25 trials in which no evidence of improvement was seen. The main steps in progress came at trials *26*, *36*, and *54*.

Response re-learned after a short interval during which the fish was subjected to disturbance. Main improvement at trial *10*.

Fish D5. *Efficient learned response*, though early trials produced the most inefficient performances of any fish. Important sudden change of behaviour, from which point onwards rapid improvement occurred.

Fish D6. *Unexpected efficient response by indirect route.* Glass obstruction with black band at its edges, which was found to make no difference.

Fish D4. *Efficient learned response* eventually established, after the first period of improvement had been nullified by a bad lapse. Early on a consistent method of solution was adopted, but it was not established. In the later response the actual movements of the fish still varied.

Fish D3. Efficient response not established, though this appeared eventually to be coming on when the trials were abandoned at the 83rd. Response nearly established much earlier on, but a very striking lapse set in.

Fish D2. No response established in 45 trials, though one period of steady improvement was passed through.

Fish D1. No response established in 45 trials, though at one time it looked as if one was developing. This fish was a steady worker, and its behaviour remarkably uniform. A change to the squared glass obstruction after trial *45* produced a striking effect, showing that something had been acquired.

Glass with Meshwork of Scratched Lines.

Fish D7. *Efficient response established.* Note that the method was different from any established, or even partly established when the obstruction was plain glass.

Fish D8. *Efficient response established*, as in D7, but not so readily. This fish a more erratic performer.

Fish D1. *Efficient response given* after change over from plain to squared glass. (Evidence of similar phenomenon in case of D3.)

DETOUR OF 4·2 CM.

Plain Glass.

Fish B. *Efficient response* soon established. When transferred to the 6·5 détour, gave an efficient response at first, but lapsed badly.

DETOUR OF 8·5 CM.

Glass Pot with Black Meshwork.

Fish D9. *Efficient response* soon established.

Consideration of what is implied by the Term "Efficient Response."

The training, it is important to remember, involved not so much the acquisition of an altogether new response, but the *modification* of a strongly established natural response—the movement towards a closely situated food-object. The fish had to acquire the habit of moving round to one side to reach the food instead of swimming straight at it. It is necessary, before the method of acquisition of this habit can be discussed, to examine what is known of the basic response, whose presence is a fundamental condition to the subsequent modification of behaviour. Consideration shows that it is not such a simple act as may at first appear.

(i) It is clear that the simple feeding response—the movement up to food-object preparatory to snapping at and swallowing it—is guided by the visual sense. Ample evidence for this has been procured. The olfactory and gustatory senses are evidently brought into play at close quarters, but this fact is irrelevant to the present discussion. The fish can be dependent on its optical receptors alone in discriminating the food-object at a distance, and in controlling its movements towards it. The response which is to be modified is a visual response directed with relation to the " object " which we must suppose is represented in the fish's visual field.

(ii) The movement which the fish performs, though it may be a simple forward motion straight ahead, implies a motor co-ordination of swimming movements. As a simple fact of observation, if the food-object moves, the fish will adjust its movements to the correlated change in its visual field. The ability to do this has been ingrained or acquired during the fish's normal life, and exists before the experiments are started. A high degree of capacity to co-ordinate its movements is possessed by the fish at the outset of the investigation. We can therefore further add that the movements which make up the whole response are directed towards keeping the fish orientated in the direction of the food-object, as forward motion is maintained.

(iii) If an attempt is made to summarize the component events in the series which comprises the response, at least the following must be found significant. (*a*) Food object is somehow differentiated in the total pattern of stimulation of the optical receptors. (*b*) Direction of movement is altered to bring this visual object into a certain relative position ; and (*c*) movement is continued and direction is adjusted, so that the visual object maintains its relation, but becomes increasingly larger. (*d*) Contact is established, swallowing actions bring the food into the fish's mouth, etc.

Further attempting to express these events in terms of neural activity, we may re-write them as follows. (*a*) Stimulation of retinal cells, giving rise to an excitatory pattern in the sensory centres of the brain. (*b*) and (*c*) Discharge of motor activity in response to the new excitatory pattern and in adjustment to it. (*d*) Culmination of swimming movements, accompanied by a new gustatory situation with resulting motor discharges bringing about snapping and swallowing.

The neural co-ordination is adequate to the task of producing a unified action (as it appears to observation), involving the integrated activity of the whole fish. If this neural integration is a reality, then it is evident that something has been left out : only the *main* neural events have been mentioned. Coincident with these are doubtless other, subsidiary, though maybe none the less important, neural reactions. Since the activity of the whole fish is involved, something is going on, whether of a stimulatory or inhibitory nature, in the neural pathways not concerned in the main reaction. It is to be inferred that these are of a kind which secure an integrated pattern of neural activity through the whole fish's body, and that habit will have established the most adequate possible. Among the subsidiary reactions those of the visceral system are no doubt important, assisting to maintain the "food perception" situation, and making ready for the discharge of digestive and gustatory reactions. On the whole, in a healthy fish, they will have come to be such as to maintain an appropriate harmony throughout the body, as well as to maintain an appropriate tension which will ensure that the animal reaches its objective in a normal effective manner. If the fish is temporarily frustrated in its movements this neural tension will be maintained. It is perhaps not going too far to postulate that nervous discharges are such that a state of physiological equilibrium is achieved at the culmination of the act, and that, if the movements are frustrated, new nervous discharges will originate maintaining the state of neural tension for a longer or shorter time, until the culmination is reached.

In short, since the activity of the whole fish is involved, the neural processes concerned are seen to be of a complex nature. Mere interference with the performance of the normal reaction will show indications of this complexity. The apparent simplicity of the act is typical of organic systems in general : they degenerate into a welter of complexity when their functioning is obstructed.

Attention has been drawn to the possibilities of subsidiary neural activity. This may play an important role in establishing physiological "states" with which are associated psychological states such as "satisfaction." It is quite possible that the association of motor responses with states of this type may lead to their establishment at the expense of others without such association. In problem learning a basis may be found for interpreting Thorndike's Law of Effect (p. 547).

(iv) To direct observation, at least, the response has the appearance of a unified action. If analysis reveals a complex of nerve reactions, it is evident that some account must be taken of the manner in which the elements of the complex are co-ordinated. No doubt in the main this co-ordination is developed by the type of neural association that has been revealed by the work on conditioned reflexes and responses. Association may be responsible for establishing, or maintaining once established, processes such as the following. (*a*) The linking of certain sensory or excitatory patterns with certain motor reactions—thus a change in the position of the food-object in the visual field may come readily to bring about a corresponding change in the direction of the fish's movement. (*b*) The linking of successive motor reactions ; a certain reaction *A* may tend to make for an increased readiness of *B*, so that the performance of *B* becomes linked to that of *A*, irrespective of what changes may be going on in the centres of sensory excitation. (*c*) Certain motor reactions may well, as Washburn (1928) suggests, become associated with certain physiological states, akin to those which accompany emotional states in higher animals. (*d*) If the food-object is kept in the same relation to other objects in the sensory field, the response may acquire an association to these.

Co-ordinated elements in the neural activity of the fish are clearly of first importance in maintaining the unity of the response against influences which tend to disturb it, or in the development of a more "complex" response if the conditions are modified. Various of these processes may play an effective part in the establishment of an efficient response when the fish, as in these experiments, has to make a detour to reach the food.

The main point to be stressed is that when an obstruction is placed in the fish's path, and when the fish has re-established what we describe as an "effective" response adapted to the new conditions, the change that has taken place essentially involves a re-adjustment of the disturbed balance. If new co-ordinations come to be established, it is on the basis of those which existed at the outset.

Consideration of the nature of the "natural response" has thus inevitably introduced the conception of an "acquired" response adapted to altered external conditions. The features that should characterize an efficient acquired response are already apparent. The two primary observable criteria are as follows. (i) It is performed with a minimum of hesitation and maximum of integration—approximating to as uniform an act as the particular individual fish is capable of giving. (ii) The efficiency of performance is stabilized, and a uniform series of rapid times is shown in the learning curve. Applying the first criterion to the special conditions of the experiments described above, we have regarded the following characteristics indicative of an efficient acquired response: (i) immediate turning leftwards away from the obstruction; (ii) persistent leftward movement for a certain distance, far enough to take the fish past the obstruction and leave it an open path to the food; and (iii) the whole response performed as one continuous act.

DISCUSSION OF LEARNING SHOWN.

Consideration of the Learning in the Light of Current Theories.

In this section we have to enquire how far the above results are explicable in terms of certain hypotheses which have been brought forward to interpret learning phenomena of the type with which we are concerned. Generally speaking, these hypotheses, even though they may have been dignified by the name of Laws, are at best generalizations which apply under certain conditions within certain limits. Consequently it should be understood that if the application of any to our present results is criticized, it is not to be implied that the hypothesis itself is attacked. The conditions may not have been suitable for the phenomena which it generalizes to have become manifested. What is intended, however, is that the relevance of these hypotheses should be tested in relation to the actual cases of learning which were observed.

The "Law of Effect."

It is perhaps most appropriate to treat first an explanation—or rather an approximation to one—which originated from the pioneer investigator in this field, and with certain obvious modifications might well apply generally in spite of the various criticisms that have been levelled against it. The essence of Thorndike's "Law of Effect" is that when, at first, an animal is unable to give an effective response to a situation which evokes action, and gives varied movements of a "trial and error" nature, after a time movements will become established which lead to a *state of satisfaction*, at the expense of others which do not. Successful movements are thus "stamped in" for the very reason that they have been successful, while "useless" movements become "stamped out" because they fail in this respect. Thorndike's own method of formulating this hypothesis is open to the obvious criticism that he is confusing physiological and psychological terms, but it seems that this difficulty can be removed by replacing the term "satisfaction" by one indicating some correlated state of neural (? and humoral) excitation. It seems quite feasible to maintain the Law of Effect on a purely physiological level.

It is supposed, then, that successful movements, by some process of association, are stamped in through their connexion with states of neural excitation accompanying the "attainment of the objective"—achieving a means of escape, reaching a food-object, or whatever it may be. It is, of course, only a first step towards anything that may be considered an *adequate* interpretation; but it is worth while to examine our results and see if they show any indication of complying with this hypothesis. If they do not, there are no grounds for pursuing this line of interpretation any further.

Each fish's performance has been critically studied, and an attempt made to trace any possible influence of successful movements in early trials on the performance of trials which follow, and on the development of any effective response that may be formed. It would be laborious, and unnecessary, however, to recount the details of this examination; for much of the data has to be set aside as of "neutral" character. We shall confine consideration to the main features which have emerged.

(1) Data have been abstracted showing the relation between methods of solution achieved in early trials and the increase in efficiency of subsequent performances. It is seen (*a*) that successful solutions in early stages do not necessarily result in the establishing of the reactions which have led to that solution: that, moreover, methods of solution may suddenly become established which have been rarely or never given before, or, if attempted, have been relatively unsuccessful. (*b*) Also the occurrence of successful solutions does not necessarily lead to an increase in the efficiency of subsequent trials, and increase in efficiency can occur when previous performances have been too varied to give any grounds for expecting immediate improvement.

The frequent early success of the "left-turn" reaction, and its failure to provide the basis of an established response, provide the best instances.

In fishes D1, 2, and 3, the left-turn movement was given from the start, and led to a solution more readily than any other response to the obstruction. Yet it did not lead to a learned response. In the first two fish it dropped out in a surprising way. In fish D4 the movement, on the whole, proved very effective; yet for a long time was only occasionally given, and did not appear at all frequently until an efficient response had been learnt by another method.

These four fish are considered together, as they did not develop a learned response within the first 45 trials. It is important to notice, however, that D3 quite early on came to give many highly efficient performances, though the efficiency was not established; yet the successful trials showed no influence of the early successful left-turn movements. D4 eventually learned satisfactorily, and will be considered again below.

Among those fish which succeeded in acquiring an adequate response comparatively quickly, at any rate D7 and 8 (with the squared glass obstruction) established a response on a movement that had been successful from the start—the " left-turn " movement, in fact. In other fish the situation is more complicated, owing to the fact that more than one type of solution proved effective in the period before efficiency had been achieved. But these provide interesting test cases. Each of them will be considered separately.

Fish A, after it had begun to show improvement, was for a time, so to speak, torn between two conflicting methods of solution—the left-turn-and-right-wheel as opposed to the sideways movement down the glass. The latter, before long, predominated. While there is nothing of special significance in this case taken by itself, it shows agreement with all other instances in the fact that, when the obstruction is of plain glass, the left-turn-right-wheel movement fails to become established in spite of its effectiveness.

It also leads us to the case of fish D6, in which, during the earlier trials, two, and only two, methods of solution were achieved. One of these, again, was the left-turn movement; the other was a withdrawing followed by a right-turn taking the fish into the right-hand regions of the tank, from which it eventually approached the food on the far side. The former movement was not often given, but, when given, led at once to a solution in six cases out of eight. The latter led to a solution after a much longer interval, and by a more circuitous route: *yet it became an established response*, the other completely dropping out after trial *12*. In this case, then, where the fish solved the trial by two alternative methods, the most laborious and, at first, inefficient was established at the expense of one that was far simpler and quicker.

The performances of D4 and 5 are considered below illustrating other phenomena of importance. In them it is seen most clearly that efficiency of performance can be established in absence of uniformity of the actual movements given. In other words, learning can still come about even *before a definite predominance has been established between alternative methods of solution.*

It seems definite enough, from the above evidence, that, in so far as the " success " of certain movements leads to their affecting the performance of subsequent trials, certain types of movement (e.g. particularly the left-turn movement) are far less effective in this respect than others.

(2) The case of fish D5, supported in some ways by D4, is of sufficient importance to warrant a more detailed résumé. This fish, it will be recalled, produced the best learned response to plain glass, although its early performances were the worst given by any of the fish (pp. 526–528).

It was prone to wander about the tank, and for the first 12 trials, during which it showed but slight inclination, if any, of tendency to improve, the solution was usually arrived at by the fish eventually *happening* to get into the part of the tank in which a free path to the food was possible. In trials *1*, *3*, *7*, and *8* it swam to the food from corner D; in *2* and *4*, it swam up from the back (region A); in *11* and *12* it swam round the edge after withdrawing to the front of the tank. Only in *5* and *9* was a solution given involving a continuous movement from the original position—a left-turn-and-right-wheel movement, as it happened. At *13*, however, it eventually solved the trial for the first time by working leftwards down the glass, making frequent contact with it until the edge was reached. The striking feature is that from now onwards all trials were solved by a method resembling this one. The chance methods, and the one given in trials *5* and *9*, dropped out completely.

The main characters of the new adopted method of solution were (i) that the fish bore leftwards and made contacts with glass as it did so, and (ii) that it never withdrew from the glass for more than a short distance in the movements that led to the solution—in fact, it gave up altogether making random movements to the other parts of the tank; and (iii) complete right or left turns no longer feature in the fish's response to the glass obstruction. Though, within these limits, the fish's movements still varied considerably, there is decidedly enough in common between these solutions to contrast them with all those given previously. It may be noted that a conspicuous change in the fish's behaviour coincided with the onset of a rapid increase in the efficiency of the response. Are these two effects to be related?

It may well seem that an interpretation on the lines of the "Law of Effect" can be applied. As a result of "trial and error" behaviour, the fish, at the end of trial *13*, happened to hit on a "satisfactory" method of solution. This method of attacking the problem became in some way "stamped in," so as to affect the behaviour of all subsequent trials. It so happens that it perhaps did so more effectively than might have been expected; but this fact would enhance rather than vitiate the argument.

It may at once be asked why the solution of *13* should have had such significant effects as contrasted with the solutions of previous trials. For the moment, however, let it be assumed that this has happened, so as to give the theory an adequate chance. We must consider in somewhat greater detail what the effects actually were.

From trials *14* to *23* learning progressed rapidly. The habit of making random movements away from the obstruction suddenly disappeared after *13*. The only vestige remaining was seen in a tendency to make occasional short withdrawing movements from the glass obstruction, but this tendency had almost completely vanished by *21*. The fish persistently worked at the glass, and showed increasing inclination to bear leftwards, until eventually getting far enough to the left to pass the edge and reach the food. Both the frequency and efficiency of leftward movements increased.

But, though the general method of tackling and solving the problem was now constant, *the actual movements involved in the solution still varied considerably*. Thus in *13*, *14*, *15*, *17*, *19*, and *20* the fish kept more or less orientated to the food, withdrawing a little before passing the edge: in *18*, *23*, and *25* it had made a half-left turn and was orientated towards the edge of the glass; in *21* it passed the edge without withdrawing at all. Good performances (marked by shortest times and least hesitation) did not depend on the method of solution. It was not until after *25* that the method had become approximately constant. It is apparent, therefore, that the fish acquired the habit of giving an efficient performance *before* the actual movements whereby it was effected had become stabilized. Such stabilization as was attained came later.

Evidently, then, whatever had become "stamped in" at trial *13* was not the actual movements involved. It appears, therefore, that in so far as the Law of Effect may be said to hold good in this case, it did not act by the establishing of certain specific motor responses. If the solution of *13* produced any permanent effects, these must have been of some other type. To this question there will be occasion to return later.

Interesting supporting evidence is derived from fish D4. This performer, after a considerable period of erratic behaviour (during which, however, some excellent trials were performed), eventually acquired a satisfactory stable level of efficiency. The most conspicuous feature in the development of this response is that, as in fish D5, but in an even more marked way, the actual method of solution continued to vary long after efficiency had been attained.

Consistently good performances were given between *49* and *69*, in which successive 5 trials averaged 22″, 17″, 15″, 15″ respectively. Three distinct methods of solution, however, persisted. The efficiency of the general response, therefore, did not depend on the stabilization of the motor reactions involved.

There is little indication in this fish that the "Law of Effect" was operating to any extent; but if some process of this type was responsible for establishing the response, the same conclusion must be drawn as above—it did not act by establishing specific motor responses.

These examples have been considered in some detail as they illustrate most clearly features of which indications were secured in several other fish.

It is to be concluded, then, that if movements which lead to solving the trial cause any neural changes of a " stamping in " nature, these are not connected with the motor paths. The possibility must not be overlooked, however, that such changes may affect that part of the neural mechanism which is involved in the co-ordination of sensory stimuli. This point will be taken up afresh after other evidence has been considered.

The Connexionist and Associationist Hypotheses.

Attempts at interpreting learning phenomena in terms of the physiological properties of nerves and nerve reflexes lead first to a somewhat elementary type of interpretation which may be distinguished as the " connexionist " hypothesis. It is based on the premise that a neural connexion once made is more readily available on another occasion. To what extent this generalization is justified is not by any means clear, in spite of the fact that it has been widely held. Perhaps the recent demonstration of " facilitation " phenomena in neural reactions of certain invertebrates by Pantin (1935, 1936) provides the best experimental data so far available. It is sufficient, however, for the present purpose to accept the fact that this effect may truly occur in the central nervous system of vertebrates, and that the hypothesis could be justified on purely physiological grounds. Now, if this is so, it is evident that a type of learning will result, due essentially to a facilitation of certain nerve connexions, accompanied perhaps by inhibition of others. This will have come about merely through repetition of the behaviour-act.

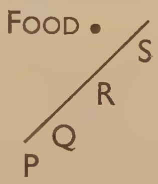
The question, however, whether detour learning is adequately interpreted on these lines is another matter. In the first place no facilitation effect is to be expected unless the reactions given in successive performances reach a certain level of uniformity ; and it has been seen above that improvement in the fishes' performances did not wait upon standardization of response. More serious still is the obvious difficulty that wherever one out of several alternative responses has to be established, something more is required—something that takes into account the fact that a certain response (or group of responses) is more appropriate than others in the " success " of its outcome. It is at any rate clear that unless the fish performs the same sequence of movements in the solution of each trial, the process of facilitation does not, so to speak, have a chance.

As an illlustration the case of D6 may be cited. The movements of this fish were unusually stereotyped. After the twelfth trial the same sequence of movements was given in each trial : the fish passed round to the right and reached the food from the far side of the tank. With successive trials the speed and efficiency with which the course was covered gradually increased. Thus the total time taken over the trial fell from an average of five minutes to a final level of about 45″. Now this increase of efficiency after trial *13*, once the habit of taking the path had become established, could well have been due to the facilitation of motor connexions, tending to integrate the sequence of movements. But—and this is the crucial point—facilitation could scarcely have had anything to do with the original "choice" of the particular route taken, as opposed to other possible responses—in other words, with the first acquirement of the habit.

Of the fish given the plain glass obstruction, fishes D1 and 3 afforded the most ample opportunity for the working of this process, as they tended to react in a uniform manner. Nevertheless, no efficient response was established in either. On the other hand, the performances of fishes D4 and D5 varied a good deal, and would scarcely have permitted neural facilitation to play more than a very subsidiary role. Yet both developed an efficient response.

It is quite unnecessary to dwell at any further length on the inadequacies of a simple connexionist interpretation. The facilitation of neural pathways cannot itself account for much, unless considered in conjunction with a related process—the *association* of contiguous pathways.

The association of motor pathways can be conceived as occurring in a manner characteristic of conditioned reflexes. If a conditioning process is at work, and if no assumptions are to be made that go beyond legitimate inferences from experimental results in this field, it is not a difficult matter to deduce the course that learning process, in these cases, should take. There is only one way in which a straightforward conditioning process could have produced the effective detour response: namely, through a linking of certain of the independent motor reactions, at first given at random in response to contact with the obstruction, by backward association with the primary reaction of swimming up to the food.



The established unconditioned response *A* (given to situation *A*) with which others may become associated is the final swimming-towards-and-snapping-at-the-food from a position P, clear of the obstruction. The first step will be that the fish in position P (situation *A*) becomes habituated to swim straight to the food from this point. "Being in position P" thus becomes, by a short step of backward association, conditioned to the final movement to the food. Carrying the process back a step farther, "being at Q" (situation *B*) becomes associated with movement to P (response *B*); similarly from a position R the fish will come to move to Q. Finally, the process of association will be carried back to the starting-point, S, where the fish first encounters the obstruction; and of various responses the fish may at first give in this position that one will eventually become established which leads it to position R, then on to Q, then on to P, and so round to the food.

The course of learning, then, would take the form of a process of backward association. The observable effects should be clear enough: for the end part of the detour would be learned first, and the beginning of the final integrated response established last. The experimental results can yield crucial evidence on this point. If they show no indication of the above deduced effects, then learning by motor association must be ruled out of question.

It is not suggested that this interpretation is either one to be expected or one which suggests itself as plausible. A little consideration will show a certain artificiality, as well as raise doubts on whether its application, if permitted by the facts, would not raise more difficulties than it removed. Nevertheless, were there indications that the learning progressed in this way, an opening would still be left for the possibility of a fairly straightforward explanation in terms of conditioned response, and it is obviously necessary, for the discussion which follows, to consider every aspect.

For the purpose of investigating this point the fish's response was conveniently divided into three phases;—(i) movements against the glass immediately opposite the food, in attempts at reaching the food direct; (ii) leftward movement taking the fish down the face of the glass plate (or parallel with the face) to its far edge; (iii) rounding the edge of the glass plate. When the most efficient integrated response had been acquired the first phase was reduced to two or three seconds, and there was no return to this position once leftward movement had started; the second phase involved a continuous movement down the glass as far as the edge without hesitation; the third phase involved movement round the edge as soon as the fish had reached this position. The acquirement of efficiency in each of these phases of the response was open to examination.

The interpretation being tested necessitates, strictly speaking, that acquirement of efficiency in the third phase should precede *any* general increase in the second, and that the second and third phases be performed as one unified act before there emerge any signs of increase in the first.

The results obtained were altogether different. Acquirement of efficiency, both in the response as a whole (as the learning curves indicate) and in the separate phases, proceeded irregularly. But there was no question of progress in one of the two earlier phases being arrested while efficiency developed in a later. On the whole, increase of efficiency in all three phases progressed together, often sudden improvements in one coinciding with improvement in another.

But it is still possible that secondary influences may have caused a certain increase in efficiency of the earlier phases while the latter were as yet imperfectly integrated. It is therefore still necessary to examine whether later phases show any sign of merely being *in advance* of the earlier. In the Appendix (p. 568) is summarized such data as bear on this point. It is seen that not even here is there the least indication of the effects which the hypothesis of backward association requires. For instance, efficiency in the case of fish D5 was established in the first, second, and third phases consecutively—in a forwards, not backwards, direction. The special case of fish D6 is particularly illuminating: the fish found the greatest difficulty over the last section of its circuitous detour, and never, to the end, really acquired efficiency in passing it.

It is therefore quite evident that the learned responses were not being built up in a backward direction from the completion of the trial. This rules out the possible interpretation that learning was effected by a process of backward conditioning.

We reach, then, the conception that processes involving the facilitation and association of *motor* paths could not have produced the effects observed in our cases of detour learning. Any attempted interpretation on these lines proves inadequate. It will be noted that the evidence here brought forward is quite different from that which had already led us to reject the possibility that successful solutions served to " stamp in " the specific movements involved.

Thus one conclusion which has emerged, reached by two independent lines of argument, is that the development of an efficient response to the obstruction was *not* primarily a matter of the linking up of certain movements, i.e. of establishing a motor habit.

Improvement in Performance due to Changes in " Sensory Organization."

Learning which involves the affector processes.

The methods of interpretation hitherto considered have one important feature in common: they take no account of possible changes in the *affector* processes concerned in the fish's response. We have merely considered the possibility of associations having become established on the *effector* (motor) side —as a result either of repetition, or of association with some general neurological state produced by relief of tension, or of backward association from the final successful movement. As these possibilities have been ruled out, attention must now be turned to the main alternative interpretation.

Some of the more familiar learning phenomena in animals belong to a class in which the animal, to speak in ordinary language, comes to " detect " certain relations in its surroundings to which it was previously indifferent. In strictly physiological terms, it is in the affector processes of the response that the essential change occurs. If there is a change in the responses given, it is because a new state of central excitation has arisen, and the new state of excitation produces a new response.

Elementary examples are provided by certain simple conditioned reflex and response experiments. In some, a newly applied " stimulus " (or " stimulus complex ") acquires the excitatory properties of another stimulus through association with it. The former, " stimulus " A, may formerly have had no conspicuous motor effect, or it may have produced a definite response which is inhibited and replaced by that primarily produced by the latter (unconditioned) " stimulus " B. One aspect of this phenomenon is that a change occurs in the excitatory effects of " stimulus " A.

In other cases, rather less elementary, the animal, giving primary response X to " stimulus " A, is conditioned to give that response to B, but to react negatively to C even when A and C are combined. These are the familiar " choice "experiments, from which the " multiple choice " experiments are a special development. Usually a particular visual object of a certain colour, size, or shape, is associated with the primary " stimulus," i.e. food-object, while another object of contrasting colour, size, or shape, is set against it, often (though not necessarily) associated with a primary " stimulus " causing a negative response. But " stimuli " of a visual nature are not the only ones on which such responses can be built ; similar results are obtained involving auditory, tactile, gustatory, and other sense receptors. By such experiments the capacity of the animal is tested for " discriminating " colours, shapes, tones, and various other " sensory " properties. The aspect of this choice-experiment conditioning which we have here to note, is the fact that the animal comes to " detect " a certain contrast, or, more generally, a certain relationship, in its sensible environment, by which, as far as the particular reaction under consideration is concerned, it was primarily unaffected. From the fact that no *new* motor reactions are involved, it is evident that the development of these various conditioned responses is primarily a sensory, or, more strictly, an *affector* phenomenon.

The work of Bull (1928–1934), Herter (1929, 1930), and others, has fully established the ability of teleost fish to develop conditioned responses of various types. With this knowledge, one may enquire whether detour learning, and, more particularly, the manner in which it has been found to occur, is predictable ; and if not, what additional factors or conceptions have to be introduced in order to account for it.

If attempts are made to find the points of comparison between detour learning and typical conditioned response effects, or to express the former in terms of conditioned reflexes, it is soon found that the problem is by no means straightforward. If it had emerged that the detour learning occurred by a process of backward association, the phenomena might have been considered directly comparable, the detour learning appearing as a chain-reflex (or, more strictly, chain-response) effect. But this has been shown not to be the case (p. 554). If, on the other hand, the detour learning compares with the conditioned response in depending on a specific change in the affector processes, then it differs in certain important respects, which at once place it on a higher level of organization, or at least of complexity. The main difference is that a new and more complex motor response develops, and not merely a change over to an alternative response previously given by the animal in other circumstances. If this is to be explained on the grounds that the animal comes to detect some "new" relationship in its surroundings (e.g. spatial and functional relations between itself, the obstruction, and the food-object) in the same sense as this may be said to occur in choice-conditioning, the situation is not in any way simplified. In choice-conditioning the "new" relationship, which the animal, so to speak, is conditioned to detect, is always a straightforward contrast providing stimuli which the sense receptors of the animal are directly capable of analysing.* But the relations which the animal would have to "learn" to detect in acquiring an efficient detour response must evidently be of a more subtle kind, and it would appear that considerable ability for producing a differentiated field of sensory excitation would have to be conceded to the animal. There would appear to be a more highly developed capacity for co-ordinating sensory impulses than might be expected, or than our present knowledge would entitle us to assume.

While, then, conditioned response experiments do not, at first inspection, provide a ready interpretation of detour learning, they do nevertheless demonstrate certain phenomena which are significant for our purpose. The first of these is that associations between nervous paths, at first functionally disconnected, may develop in an orderly and predictable manner; the second is that such associations may develop centrally in that region of the central nervous system which functions in co-ordinating the impulses transmitted by the peripheral receptors. They provide a certain neurological basis for pursuing an attempted interpretation of detour learning as an affector phenomenon.

The affector processes which initiate any given response include both events which occur peripherally in the sense receptors, and those which occur centrally in the sensory centres of the central nervous system. There is first a process involving an analysis of external energy-exchanges into aggregates of unit stimuli, and secondly a re-synthesis of the aggregates of impulses reaching the sensory centres. The mechanisms underlying these complementary functions constitute the affector system. That a distinction should be recognized between sensory analysis and sensory synthesis seems inevitable not merely on morphological grounds, but also as an outcome of the conditioned-response work. The conception, in fact, is derived from Pavlov :

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* See below, p. 558.

> " . . . the nervous system possesses on the one hand a definite analysing mechanism, by means of which it selects out of the whole complexity of the environment those units which are of significance, and, on the other hand, a synthesising mechanism by means of which individual units can be integrated into an excitatory complex. Thus in studying the nervous activity of the cerebral cortex it is necessary to deal with two . . . distinct phenomena, one involving a neuro-analysis and the other a neuro-synthesis."*

This generalization was intended to apply to Mammalia—vertebrates possessing a cerebral cortex. Nevertheless other vertebrates, as well as some invertebrates, possess centres in the central nervous system associated with afferent nerves and it appears from simple observation that the function of sensory organization—hence neuro-synthesis—is possessed by these animals, however limited that function may be. At the very least it is possessed by teleost fish, which prove capable of producing many of the conditioned reflex phenomena demonstrated in mammals.

Accordingly—to return to the learning problem—if a change occurs in the affector processes, this may involve either the process of neuro-analysis or that of neuro-synthesis. Changes of the first category could involve little more than an alteration of the threshold of excitation of the sensory receptors, though such changes might conceivably have far-reaching effects on behaviour. The second type includes other cases in which a change in the central excitatory complex results. Such could arise through the development of a new neural association. One of its essential features is that it occurs through causes independent of the process of neuro-analysis : it may occur although the external conditions, the stimulation of the sense organs, and the impulses transmitted by them, remain identical.

Since mere changes in the threshold of excitation of the sense receptors could not possibly account even for the most elementary conditioned reflex, to say nothing of detour learning, we may proceed straight away to consider the latter as due to a change in the process of neuro-synthesis. That we are justified in assuming that changes can occur at this stage may be seen by referring back once more to the more elementary conditioned response effects mentioned above. It has been pointed out that these are to be regarded as affector phenomena, occurring centrally, which is the same thing as saying that they involve the process of neuro-synthesis.

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* *Conditioned Reflexes*, trans. by G. V. Anrep, 1927, p. 110.

As the change in question is a matter of association of formerly independent nerve-paths, it may be accepted that the process of neuro-synthesis may be modified, under certain conditions, through certain changes which are of the nature of neural associations.

This conclusion has obvious significance in relation to our problem. It may be asked why it was not introduced at the start of the discussion, or at least in the section above (p. 552) dealing with the associationist hypothesis. The fact remains, however, that the type of modification that appears necessarily involved in detour learning is somewhat different, in some respects more complex, than any indicated by conditioned response experiments. It was not justifiable to attempt this line of interpretation before others, which had the appearance of being more straightforward, had been tested.

The first stage of the analysis of our problem brought us to the significant conclusion that the learning shown was not primarily a matter of the development of a motor habit. Having seen that ample precedent exists for doing so, we have now to proceed to test the hypothesis that the learning has resulted from a modification in the process of neuro-synthesis, i.e. in the manner in which the sensory impulses are integrated.

It will first be necessary to consider a body of evidence of a positive character that at least encourages us in pursuing this line of interpretation.

Effects of visible changes in the surroundings.

The evidence now to be discussed illustrates perhaps the most important feature which has emerged during the course of the experiments, namely, that *changes in the details of the conditions presented to the fish were capable of exerting marked effects on the course of learning.* The changes in question concerned visual characteristics of a type the fish proved able to detect, i.e. affected its responses. Also, their *only* effect on the fish was through the visual sense: they did not in any way directly influence the response movements, or require *different* response movements, as would, for example, spatial re-arrangement of the apparatus, or changes like the setting up of currents in the water. If, then, an influence on the response, or cause of learning, could be detected, it could only have been a secondary influence of the changed pattern of sensory stimulation. The significance of this consideration will be seen later.

(i) As described above, some of the experiments were made with the glass obstruction marked with a meshwork of fine lines. The lines, scratched with a glass-cutter, half a centimetre apart, did not seriously interrupt the view through the glass. Fishes 7 and 8 were presented with this "squared" glass from the start. The former proved a good subject and was not long in acquiring an efficient response, which developed during the period between trials *10* and *20*. From *21* onwards a series of uniform efficient performances was given, averaging some 11″. This was rather quicker than fish D5, the outstanding performer among the seven fish presented with plain glass. Fish D8 showed more erratic behaviour all through, but eventually became as efficient as D7. Unlike the latter, it showed, to start with, strong tendency to wander over the dish, and for some time its performances fluctuated considerably. There is little doubt that this fish would have encountered great difficulty with a plain glass obstruction, and would probably have ranked with those fish that failed to establish an efficient response.

The evidence points strongly to the fact that the detour round the "squared" glass obstruction was more easily learned than in the case of the plain glass. This might well have been expected, since the fishes showed unmistakable signs of "seeing" the pattern on the glass, fine as the lines were. The evidence for this statement is of two kinds. (i) In early trials the fish often worked close against the surface of the glass: in moving leftwards, they usually moved jerkily from one line to another, in a manner never observed when the glass was plain. (ii) In the acquired response the fish turned leftwards before reaching the glass, at a point about 2 cm. distant, as though they had acquired the habit of bearing away from the obstruction as soon as the pattern came into focus: and this was in strong contrast both with the behaviour of other fish presented with plain glass, and with tests on the same fish when plain glass was substituted for squared. Evidently, then, the obstruction was marked with visible characteristics, and it is scarcely surprising that the fish was more effectively enabled to make the detour.

TABLE VII.

Performances of Fish D1 in Later Trials.

Trial No.	Obstruction.	Duration of trial.	Average of five successive trials.	
36	Plain glass	0′ 28″	*36–40*	2′ 26″
37	,, ,,	1′ 20″		
38	,, ,,	1′ 41″		
39	,, ,,	5′ 47″		
40	,, ,,	1′ 55″		
41	,, ,,	2′ 39″	*41–45*	2′ 21″
42	,, ,,	1′ 07″		
43	,, ,,	1′ 58″		
44	,, ,,	1′ 38″		
45	,, ,,	4′ 25″		
46	**Squared glass**	**0′ 18″**	*46–50*	**0′ 19″**
47	,, ,,	**0′ 15″**		
48	,, ,,	**0′ 28″**		
49	,, ,,	**0′ 22″**		
50	,, ,,	**0′ 14″**		
51	,, ,,	**0′ 11″**	*51, 53–56*	**0′ 19″**
52	Plain glass	3′ 0″+*		
53	**Squared glass**	**0′ 43″**		
54	,, ,,	**0′ 16″**		
55	,, ,,	**0′ 12″**		
56	,, ,,	**0′ 12″**		
57	,, ,,	**0′ 12″**	*57, 59, 60*	**0′ 14″**
58	Plain glass	3′ 0″+*		
59	**Squared glass**	**0′ 13″**		
60	,, ,,	**0′ 16″**		

But more significant still, perhaps, is the fact that the learned response given by these two fish was of a *distinctive type*, differing from any acquired by the fish which learned to surmount the plain glass obstruction. Both fishes, D7 and 8, made the detour by turning leftwards, before touching the glass, swimming left, and wheeling round the edge in one movement. This manoeuvre, as has already been pointed out, was given by all fish during early trials. In spite of its effectiveness, as again has previously been emphasized, it was never established, sometimes dropping out of the fish's repertory in a striking manner. Where, in short, the obstruction was plain glass, the left-turn movement proved impossible to establish. Yet it provided the effective response in both fish trained to "squared" glass. The conclusion seems unavoidable that the marking on the glass made for this significant contrast. This is made all the more certain by the fact that essentially the same movement is given to an obstruction which has striking visible characteristics, such as the pot presented to fish D9.

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* Abandoned before a solution was achieved.

The experiments with fishes D7 and 8 thus indicate that the meshwork marked on the glass, endowing it with a visible property, (*a*) rendered the detour learning easier, and (*b*) influenced in a marked way the character of the learned response.

(ii) The experiment of substituting the plain glass for squared glass was made in the case of fish D1. This fish, in spite of the uniformity of its behaviour, had shown no signs of establishing a learned response. The result, as may be seen from Table VII, was remarkable.

On the very first occasion the squared glass was introduced a response of marked efficiency was given, and this efficiency was maintained. The average level of the duration of the trial fell to below 25% of its previous value. That no sudden permanent change had taken place, affecting behaviour in both conditions alike, is shown by the results of trials *52* and *58*, in which plain glass was used again. In both of these trials the fish proved incapable of making the detour before the trial was abandoned at the end of three minutes. Here, then, the pattern on the glass made all the difference between a laboriously attained solution, and one approaching maximum efficiency.

A similar test was made with fish D3, and the results, as far as they go, are comparable, if not so striking. At the time this fish was tested it was beginning to show gradual improvement, after a period of very inefficient performances. The figures are given in Table VIII.

TABLE VIII.

TESTS WITH SQUARED GLASS ON FISH D3.

Plain glass.		Tests with squared glass.	
Trial No.	Duration.	*Trial No.*	Duration.
69	4′ 01″	*70*	0′ 11″
71	1′ 59″		
72	0′ 55″	*73*	0′ 16″
74	1′ 29″	*75*	0′ 45″
76	1′ 35″		
77	1′ 19″	*78*	2′ 26″

The first three tests showed a marked reduction in duration as compared with the normal controls, particularly the first. What is also of interest is that the behaviour during the tests differed appreciably from that normally shown by the fish. Most notably, there was a complete absence of withdrawing movements, which characterized all other trials. The fourth test (*78*) showed a bad lapse, and might appear to vitiate the results. It must be noted, however, that in this trial the difference in behaviour was conspicuous all the time, and the solution was eventually reached in a manner similar to that in the other tests, and quite unlike that shown normally.

The effect, then, of replacing plain glass by the squared glass, is that the detour is more readily accomplished. This is brought out in a striking way in the above records from the performances of fish D1. At the same time, as indicated by fish D3, the mode of behaviour during the trial, and the method by which the solution is reached, may be affected.

(iii) During the course of the experiments incidents were noted from time to time which indicated that features in the visible surroundings of the fish influenced the behaviour. In one case quite a trivial feature was responsible for so affecting the fish's response that the efficiency of performance was altogether impaired. This incident, which occurred in the training of the first animal investigated (fish A), is worth recording in detail.

During the second series of trials with this fish, after an efficient method of solution had been re-established, unexpected failures occurred in three trials, in which the fish failed to get straight round the edge of the glass first time. It was then noticed that a strip of white paper inserted into the groove supporting the glass plate (see description of apparatus, p. 505) was protruding a little from the groove, and ended a little short of the edge of the glass. For the purpose of testing whether the presence and position of the strip of paper had any influence on the extent of leftward movement of the fish, the paper was re-adjusted and made to protrude *beyond* the edge of the glass. The fish was again tested and now gave a perfectly efficient performance. Tests were continued, amounting to seven altogether on this particular day. The results are given below in Table IX. Situation A denotes that the edge of the glass lay beyond the edge of the paper, and B that the edge of the paper protruded beyond the edge of the glass.

TABLE IX.

Performances of Fish A, 23.2.34.

Situation.	Performance.
A	2 unsuccessful moves before frame removed at 20″.
B	*round first time* (*at 11″*).
B	*round first time* (*at 8″*).
A	3 unsuccessful moves before frame removed at 20″.
B	*round first time* (*at 7″*).
A	5 unsuccessful moves before eventually reaching food at 45″.
B	*round first time* (*at 30″, but fish by now not hungry*).

It seems clear enough that the position of the edge of the paper was responsible for the fish's failures. This suggests at once that the fish was using the visible protruding strip as a guide to the position of the invisible edge of the glass. Be this as it may, a further test showed that the learned response itself was not at all dependent on the presence of a white paper strip. The next day the white paper was replaced by light brown paper fitted well into the groove so as to be invisible from below. There was therefore nothing which could be taken as a " sign " of the edge of the glass. With this arrangement the fish gave perfectly satisfactory trials. It was thus shown that the fish had not learned the position of the edge of the glass by association with the white paper.

It is therefore to be concluded that the presence of the slightly protruding strip of paper, ending before the edge of the glass, had *distracted* the fish in some way. No doubt, this was because the fish, relying by habit on its vision, had a tendency to pick up visual clues when there was the least chance of being enabled to do so, and in this case had begun to develop an association with a clue that turned out to be a *false* one. But, however this may be, the point to be brought out is that details in the visual field can exert significant effects on the response.

The above examples illustrate how changes induced in the conditions presented to the fish—changes of kind which do not modify the detour problem, or affect the fish's response movements in any direct way, but which are detected by the fish through its visual receptors, and thus presumably affect the visual pattern to which it reacts—can affect the response in a significant manner. We have considered cases in which there is a *contrast* between two different experiments, and cases in which *changes* are introduced at some point in one series of trials. The same kind of effects are noticed in both.

Where contrasts, or changes, are noted in the response, the cause can only reside in a contrast, or change, in the sensory situation (however we may visualize or define this event) to which the fish reacts. Situation A evokes response *a*, while situation B evokes response *b*. We are not now concerned with what causes the particular characteristics of *a* or *b*. The point that must be made is that the differences observed in the response of the fish are induced in this way –by a difference in the situation which evokes them.

It may finally be observed that differences in the external conditions have been seen to exert two types of effect. First, there is the more immediate effect on the behaviour shown in the particular trials concerned. Secondly, as in the example of fishes D7 and D8, they may exert a more "long-range" influence, by affecting the selection of that form of behaviour which is eventually established as a learned response.

Detour learning an affector phenomenon.

The observational data just considered have a significant bearing on our problem. In showing that externally induced changes in the affector processes of the fish's reaction have marked effects on the learning process, they virtually demonstrate that *any* change in the affector processes can exert such effects. For those occurring peripherally are farthest removed from those that constitute the final central state of excitation through which the motor centres are activated. If, then, neural changes occur more centrally—such as in the process of neuro-synthesis (see p. 558) –they must be at least as capable of affecting the fish's performance as those induced peripherally.

Though internal changes affecting neuro-synthesis are hidden from direct observation, we have seen that it is necessary to infer their existence in interpreting the results of conditioned response experiments (p. 558). But, furthermore, from evidence considered earlier, it is concluded that they are necessarily involved in the present case. The detour learning observed involves some internal neural change: this change does not involve the motor, or effector, processes of the response (p. 559): therefore an appropriate change in the affector processes remains the only alternative.

Taken together these two main conclusions leave room for only one plausible interpretation of the learning observed. The latter assuredly depends on a change involving the processes of neuro-synthesis. It is an *affector* phenomenon.

For some purposes it is preferable to express this reasoning in a rather different form, lest any shortcomings of the neurological concepts hitherto employed should be supposed to vitiate the deductions.

We may consider the situation (to which the animal's movements are adjusted and modified) as a whole, and call it the *perceptory situation.* This term is employed in its most general sense to express, objectively, the "sensed" situation to which the fish reacts, whatever it may be, whether an aggregate of stimuli, or whether something that has to be distinguished as a "gestalt" or organized pattern. The two main conclusions now may be expressed as follows. (i) The observed learning is not a motor habit; the only apparent alternative is that it involves a significant change in the perceptory situation to which the motor reactions are directed and adjusted. (ii) Changes in the perceptory situation, externally induced, can exert significant effects on the fish's response; therefore any changes in the perceptory situation, including those which may arise internally, have at least comparable effects. The final conception to which we are led is that learning takes place because a new perceptory situation arises which renders possible a more adequate response.

A picture of the process by which the wrasse learnt the detour path may now be sketched in its broad outlines. When first the food is presented behind the obstruction, the fish does not adequately prehend* the relations of the objects external to it, or adequately co-ordinate its sense impressions to enable it to give an effective response. It makes various ineffective movements which tend to become increasingly random, until by chance it gets into a position from which it can reach the food. With repetition of the situation, sooner or later a change occurs in the way in which the fish prehends its surroundings, and a new response is given (to what is essentially a new situation). The change, further, is such that the fish can give a more adequate response, enabling it to circumvent the obstruction, and so evidently involves a prehension of some significant relation, not detected before, between the fish itself, the obstruction, and the food. In the end the main relations are sufficiently well prehended to enable it to make the detour with a maximum efficiency.

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* This term is introduced to express the relation between the animal and the elements of (or relationships in) its surroundings which it proves able to differentiate. It may be defined as equivalent to the term "detect" shorn of its subjective implications. An animal can be said to "prehend" an object or contrast with no commitment as to whether the event involves consciousness on the animal's part.

It is perhaps not so much the fact that the problem of detour learning appears to be essentially a problem of sense-perception which is important, as the evidence from which this judgment is derived. Investigators who adopt the theories of the Gestalt school have stressed the probable importance of changes taking place in the perceptual field (see, e.g. Wheeler, 1929). As mentioned at the outset (p. 501), E. S. Russell has drawn attention to this aspect of the problem, and has suggested that the interpretation of simple detour learning shown by sticklebacks is rightly to be conceived on these lines. But, perhaps without exception, interpretations of this type have had their origin not so much in logical deduction from experimental results as from the metaphysical viewpoint from which the results have been described. This is not to say that the interpretations are false, but they will be unsatisfactory scientifically until they can be shown to be *required* by the results of experiment. In so far as they have hitherto been thought inappropriate may lie merely in the inadequacy of the necessary experimental data. This remains to be seen. However, since the course of the present discussion is guided by the principle of procedure from fact to hypothesis (and back again), it seems that " organismal " theories of learning (if they may so be called) are most conveniently introduced at a later stage, when the consideration of the data presented above is complete—when, in particular, the nature of the perceptory change involved in the learning has been more closely examined.

It is concluded, then, that the improvement in performance which characterizes the learning we have been studying is the result of a more adequate perception of the conditions presented to the fish. It will be noticed that this does not actually solve the problem of learning, but it does, at least, define where the problem really lies. The crucial point to be established is how the change in the perceptory field comes about, and why the change should be of the particular type found. It will be necessary to turn once again to the experimental data to discover if any light has been thrown on this problem.

I wish to express my gratitude to Dr. E. J. Allen for his encouragement and sympathetic advice given to me on various occasions during the course of this work; to those with whom I have had profitable discussions on problems bearing on animal learning, particularly Dr. E. S. Russell and Dr. C. F. A. Pantin; and to Dr. S. Kemp for reading the manuscript, and offering some helpful suggestions for its final preparation.

SUMMARY.

1. This paper deals with certain experiments on training fish (*Ctenolabrus rupestris* L.) to swim round obstructions to reach food, for the purpose of investigating how their learned response was developed. The whole question as to how learning which involves " problem-solving " is rightly to be interpreted and harmonized with our knowledge of conditioned responses, presents difficulties which have not yet been adequately faced.

2. A description is given of the results of experiments carried out on eleven fish. The fish had to learn a detour route either into a pot or round glass plates. Attention may be drawn to the great diversity in the behaviour of individual fish, both in their reactions to the obstruction at different stages of training, and in the method by which they succeeded in passing it. Some individuals are evidently more capable of profiting by experience than others.

3. As complete a record as possible was made of all performances ; and these data were carefully analysed with a view to exposing the conditions under which efficient responses developed, and to detecting any possible causal influences. The results of this analysis, of which the main features are summarized below, may be partly summed up by saying that learning could progress in spite of considerable and significant irregularities in the fishes' performances. These were such as to preclude all the more straightforward* interpretations of the learning that can be suggested.

4. No general connexion was apparent between the behaviour shown in early trials and that in later trials, when the behaviour, if not perfectly integrated, was at least more uniform. It proved impossible, from examination of behaviour in early trials, to predict whether an efficient learned response would be established, or, if established, what particular movements would be involved. The experiments in which the obstruction was of clear glass, and the detour learned with difficulty, if at all, afford the most critical tests.

5. In particular, the movements which had led to successful solutions in early trials were by no means necessarily " stamped in " or reproduced in an efficient response, if and when this was achieved. Moreover, an efficient response can be established even before the movements by which it is carried out are at all stabilized. The possibility, therefore, that the learning had arisen, in accordance with the " Law of Effect," as a result of the recurrence of those movements which came most frequently to be associated with the solution of the problem, is excluded.

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* i.e., from a physiological point of view.

6. While an efficient response was developing, the integration of the later movements did not proceed in advance of that of the earlier. The data are quite incompatible with the hypothesis that the response developed from independent movements linked by a process of backward association.

7. Since also the "connexionist" hypothesis fails to account for the facts, the possibility that the learning involved nothing more than the development of a motor-habit is now finally eliminated.

8. Only one alternative remains to be explored, namely, that the learning is an *affector* phenomenon. It would thus be associated with the synthesizing, or organizing, processes which must be assumed to occur in the sensory centres of the central nervous system.

9. A certain body of evidence is shown to encourage this view. Details in the external conditions which cannot affect the fish's activity except through the medium of the sense-organs, are found to exert considerable effects on behaviour—both on the performance of individual trials and on the trend of behaviour as a whole through a series of trials. Thus if a meshwork of fine lines is scratched on the glass plate, learning is greatly facilitated, and the movements by which the fish make the detour are significantly different.

10. The conclusion of the evidence considered is that learning is essentially due to the discrimination of some general relation in the external situation which had not previously been prehended (or "detected"). With a clearer appreciation of its surroundings the fish is enabled to give a more effective response. It remains to examine how this critical change takes place, and how its essentially adaptive character is to be explained.

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APPENDIX.

Data bearing on the Possibility of Backward Association.

FISH A.

First series of trials.

The component phases of the learned response were acquired in the following stages.

Trial *8*. Random movements to other parts of the tank mainly eliminated.

Trials *25* to *30*. First permanent reduction in time spent in attempts at swimming straight at food before any leftward movement. Fish now gets into the habit of working steadily down the glass.

Trial *36*. From now on usually moves straight down the glass and passes round the edge first time on 4 occasions out of 5.

Trial *55*. Proficiency in the above virtually established.

Trials *55* to *60*. Further reduction in the duration of the first phase, before first leftward movement, and final proficiency acquired.

There is no indication here of later movements acquiring efficiency earlier.

Second series.

The main step in the re-establishment of the learned response came in trials *B9–11*, and was marked by rather an increase in efficiency of both the first and third phases of the response.

FISH D5.

Phases of the learned response were established in the following order.

1. First phase, over which the fish hardly ever spent any length of time.
2. Second phase: the habit of moving as far as the edge of the glass plate in the first leftward movement.
3. Third phase: the habit of passing round the edge at first attempt.

Note that the integration of the response proceeded from the beginning forwards, and not from the end backwards.

FISH D7.

No one phase can well be said to have acquired proficiency before any other. Progress affected the response as a whole.

FISH D8.

This fish first became proficient at moving leftwards in a half-circle (full left-turn followed, after a longer or shorter forward movement, by a wheeling to the right), simultaneously reducing the time spent in attempts at reaching the food directly.

It was a long time, however, before it became proficient in passing round the edge of the glass on its first leftward movement. A considerable delay in establishing perfect integration was entirely due to errors made in the last phase of the response.

FISH D4.

The first phase never occupied any length of time, and the fish developed a habit of moving leftward efficiently at an early stage.

Until behaviour changed at trial *41*, when a bad lapse set in, the perfection of an efficient response only depended on the ability of the fish to pass round the edge of the glass, once it had moved far enough to the left (third phase). But consistency in this habit was not acquired during this period.

In the eventual learning which set in after trial *42*, the fish at first was taking a considerable time to reach the edge of the glass. But reaching the edge in short time did not wait upon the acquisition of the habit of moving round the edge at the first attempt. Integration of the second and third phases progressed simultaneously.

FISH D6.

The data provided by this fish are particularly instructive, as the long route taken fell into three natural stages, namely (i) withdrawal from L and passage round Q, (ii) passage through K round P, and (iii) passage through J round O.

On page 537 figures are given for the times taken for the respective stages, and it is at once apparent that the last phase was never really efficiently learned. The average times for the passage round O are consistently high.

It is quite evident that the rapid passage from Q to P did not depend on the association with an efficiently integrated passage from P to O. Still less did the habit of turning away from the food at L and rounding Q depend in any way on the complete integration of the rest of the response.

The Air Turbine Ultracentrifuge, together with some Results upon Ultracentrifuging the Eggs of *Fucus serratus.*

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With Plate II and 8 Figures in the Text.

Introduction.

Generally, the force of gravity has little or no effect upon the distribution of the various materials within cells, although they may differ considerably in their relative specific gravity. However, by means of the centrifuge forces can be obtained many times greater than gravity, which otherwise exist only on the very largest planets. Because of this fact, the centrifuge has proved to be a very valuable instrument in the study of many problems of biology. For instance, in experimental cytology and embryology, the subjects with which we are here concerned, it has been used extensively to bring about a redistribution of the various materials within the animal egg, such as the yolk, the pigment, the protoplasm and the fat. From such experiments the role of these various substances as possible organ-forming materials and as affecting cellular differentiation has been studied. Other problems such as fragmentation of the egg, viscosity of the protoplasm, membrane strengths, influence of gravity upon development, differential injury to eggs, molecular weight determinations, polarity, and the cytoplasmic components and inclusions have all been profitably investigated by means of the centrifuge.

The types of devices that have been used to generate centrifugal force in biological experiments are many and varied. For instance, we find a gradual evolution from a simple wagon-like wheel used by Knight in 1815 to study the effect of centrifugal force upon developing plants, to various types of hand centrifuges with high gear ratios, to the fly-wheel of an engine as used by Morgan (1902), to electric and water driven centrifuges, to the Sharples supercentrifuge which develops forces upward to 62,000 times gravity, to the Svedberg oil turbine centrifuge capable of developing forces upward to 400,000 times gravity, and finally to the recently

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* Aided by a grant from the Rockefeller Foundation for work on Cellular Biology.

developed air turbine ultracentrifuge, constructed of air spun rotors without bearings which give rotations of several thousand times a second and develop forces of the order of 400,000 to 7,000,000 times gravity. Forces developed by such centrifuges are limited mainly by the tensile strength of the metal of which the rotors are made. It is this latter type of ultracentrifuge that has been used in the experiments to be described below.

THE ULTRACENTRIFUGE.

Since the air turbine ultracentrifuge has only recently been applied to studies in biological work and since it promises to have a rather wide application in biological experiments, it seemed desirable to give illustrations and a brief description of it here. I shall not attempt to give a detailed explanation of the various parts of the ultracentrifuge, but only to point out its important characteristics so that the reader may have a fair understanding of its construction and operation. Those desiring to construct the apparatus will find complete specifications in the papers by Beams (1930), Beams and Weed (1931), Beams, Weed and Pickels (1933), and Beams and Pickels (1935). The cost of constructing the ultracentrifuge is very low in comparison with that of other types of high speed centrifuges.

The first investigators to use the air turbine for centrifuge work seem to have been Henriot and Huguenard (1927). However, it has been greatly modified and developed into a practical laboratory apparatus by Professor J. W. Beams and his associates of the University of Virginia.

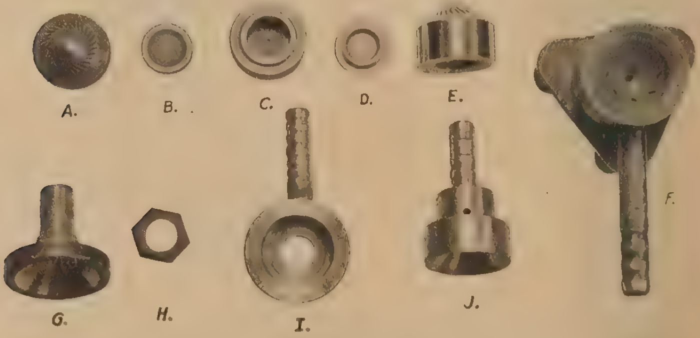

FIG. 1.—The ultracentrifuge. A, bottom of rotor cone showing flutings; B, top of cap which screws into rotor from above; C, top of rotor showing centrifuge cavity; D, bottom of cap as in B; E, side view of rotor; F, assembled stator showing stator cup and eight diagonal holes; G–I, unassembled parts of stator; J, stator with air entering from below instead of from side, as in F.

The ultracentrifuge which I have used is composed of two principal parts: the rotor and the stator (Figs. 1, 2, and 3). The rotor is a small, one and one-eighth inch diameter, all metal (steel, brass, duraluminum, monel metal) structure, shaped like a schoolboy's top, but with a cavity in the centre which holds approximately 4 c.c. of fluid (Fig. 1, A–E). However, rotors may be constructed which hold many times this amount. A small screw cap seals the centrifuge cavity from above (Fig. 1, B and D). The lower portion, or cone-shaped part of the rotor, which is grooved with a series of flutings is mounted in a cup, the stator (Fig. 1, F), also of conical shape, but of a slightly different angle so that the rotor cone touches the stator cup when not running at its top only, which is also its largest diameter (Figs. 2, B; 3, A). To start the ultracentrifuge the rotor is placed in the cup of the stator and air under pressure (2 to 150 lb. per sq. inch) is released and passes through the tube labelled "air pressure" into the stator chamber and then through the eight diagonal holes into the stator cup where it impinges on the flutings of the rotor and starts it rotating (Fig. 3, A). The air that is used to cause rotation then escapes between the surface of the rotor cone and of the stator cup, floating the rotor on a cushion of air just above the stator cup, entirely free of any mechanical contact. At the same time that air under pressure is escaping between the surfaces of the stator and the rotor, air is entering from the atmosphere through a small hole at the vertex of the stator because of the reduced pressure at this point (Fig. 3, A, labelled "stabilising air flow"). This, according to Beams and Pickels (1935), greatly improves

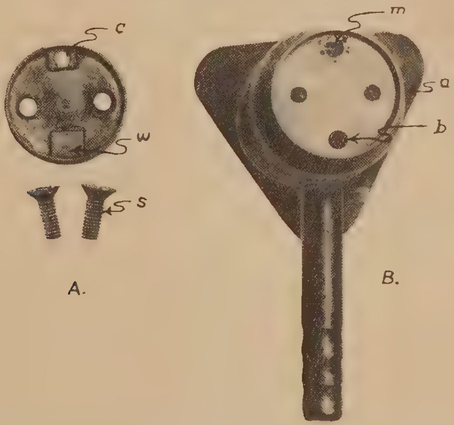

Fig. 2.—The microscope ultracentrifuge. A, detachable top showing centrifuge chamber (*c*) above and balance weight (*w*) below; machine screws (*s*) fasten detachable top into position on rotor in B; B, upper view of rotor (*a*) resting in stator and showing tube leading to mirror (*m*) with counter balance tube (*b*) below.

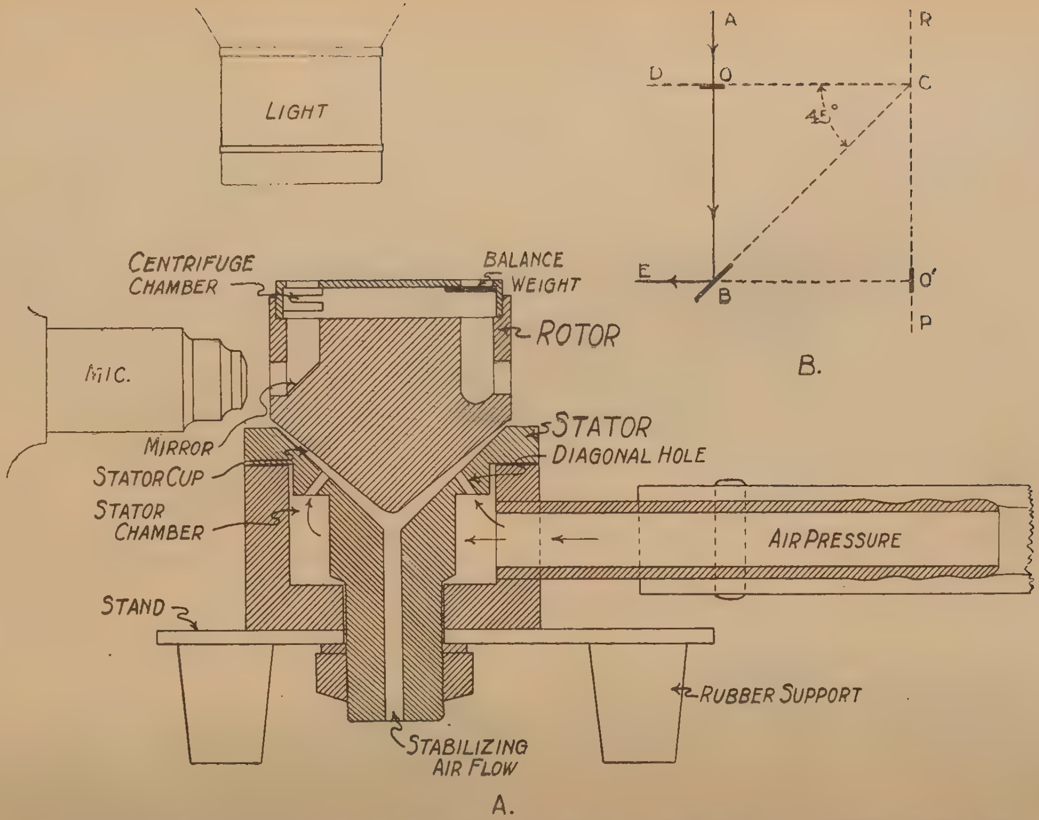
LIGHT
CENTRIFUGE CHAMBER
BALANCE WEIGHT
ROTOR
MIC.
MIRROR
STATOR CUP
STATOR CHAMBER
STATOR
DIAGONAL HOLE
AIR PRESSURE
STAND
RUBBER SUPPORT
STABILIZING AIR FLOW
A.
A
R
D
O
C
45°
E
B
O′
P
B.

FIG. 3.—A, section through microscope ultracentrifuge. Labels are self-explanatory. B, diagram showing the optical system of the rotor in A (modified from Pickels). The centrifuge chamber has a diameter large in comparison with its thickness. "B, is a small plane mirror mounted on the rotor. Light from a straight filament lamp is focused upon O so that the image of the filament lies along CD and consequently transverse to the direction of the motion of the object thus illuminated. As O then revolves about RP, it becomes visible to the naked eye or in a microscope only as it passes through the indicated position. Consequently, as viewed from E the virtual image O will appear stationary and under apparently continuous illumination

stability and helps to adjust automatically the air cushion for different air pressures, speeds, and weights of rotors. This is an important improvement over the first models in which the rotors were supported by a separate

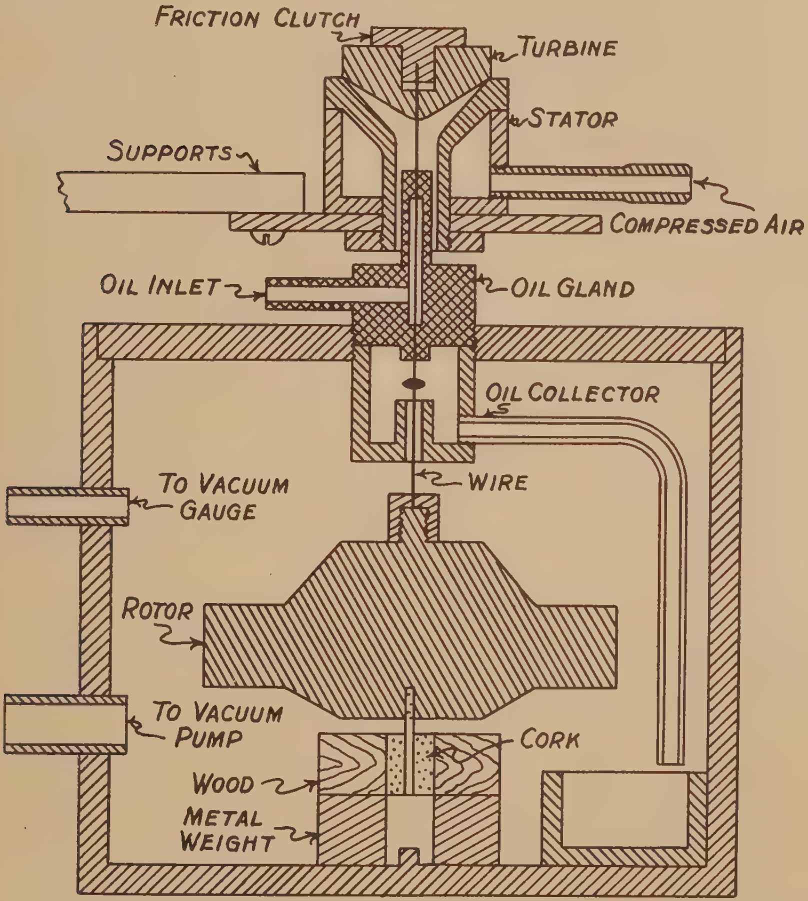
FRICTION CLUTCH
TURBINE
STATOR
SUPPORTS
COMPRESSED AIR
OIL INLET
OIL GLAND
OIL COLLECTOR
WIRE
TO VACUUM GAUGE
ROTOR
TO VACUUM PUMP
CORK
WOOD
METAL WEIGHT

FIG. 4.—Air turbine vacuum ultracentrifuge (redrawn from Beams and Pickels, 1935). In this design the driving mechanism is simply an air turbine rotor as above described (Fig. 1). From the vertex of the driving rotor or turbine a small steel wire extends downward through an oil gland into a vacuum chamber and is attached to a much larger rotor which contains a cavity where the material to be centrifuged is placed. Since the rotor which spins in the vacuum chamber is of much greater diameter than the turbine rotor, enormous centrifugal forces may be obtained.

column of air from that which was used to cause rotation. The rotor is prevented from being blown out of the stator cup by the principle of Bernouilli. The forces involved in this principle are so great at high pressures that the entire ultracentrifuge may be inverted without the rotor falling out of the stator; because of this fact, too, it is not essential that the rotor be exactly balanced. Another important feature of this type of ultracentrifuge, especially in biological work, is that the temperature does not vary in the rotor chamber over a few degrees from that of the atmosphere even though the rotor may be operating at very high speeds.

The speed of the rotor may be accurately and easily determined by the stroboscopic method and the amount of centrifugal force developed calculated. The size and shape of the rotors are subject to wide variation and Beams and Weed (1931) have described rotors in which materials may be introduced, separated, and the lighter and heavier materials collected while rotating. They have also designed rotors to observe the sedimentation velocity of particles at very high speeds. To stop the rotor when it is running at high speeds the air pressure is reduced to 3 to 5 lb., which is sufficient to sustain an air column between the rotor and the stator. When the rotor has reduced its speed (as determined by pitch), the fingers are placed about it and pressed gently against the sides until it stops. The air pressure should never be completely cut off while the centrifuge is operating as the rotor will drop down on to the stator and then jump off. Caution is urged that, when the ultracentrifuge is to be operated at high speeds, it be placed behind a suitable barricade to protect the operator in case the rotor should explode.

Another type of ultracentrifuge has recently been described by Beams and Pickels (1935) and they have very kindly permitted me to reproduce it in Figure 4. In brief, the advantage of this model over the one above described is that the rotor which contains the material to be centrifuged spins in a vacuum and may be kept thermally insulated, which is an important factor in preventing troublesome convection currents from occurring in the centrifuged liquid, especially when the rate of molecular sedimentation is being observed.*

THE MICROSCOPE ULTRACENTRIFUGE.

Recently Harvey and Loomis (1930) have described a unique and ingenious type of microscope centrifuge in which the materials may be continuously observed while centrifuging. Harvey (1934) has adapted this principle to the air turbine ultracentrifuge mentioned above. In such a microscope ultracentrifuge he was able to take clear photographs of eggs being centrifuged at 84,000 times gravity. Figures 2 and 3 show rotors adapted as microscope ultracentrifuges which were constructed for me by Dr. E. G. Pickels in Dr. J. W. Beams' laboratory. The design of the optical system differs considerably from that of Dr. Harvey (Fig. 3, B). The chamber which holds the material to be centrifuged is made of a specially treated glass (Beams, Weed, and Pickels, 1933), sealed at one end and cemented into position on the detachable top of the rotor (Figs. 2, A ; 3, A). The top (Fig. 2, A) is placed over the body of the rotor, as in Figure 3, A, and fastened in position by machine screws so that the chamber containing the material to be centrifuged is directly over the mirror. The mirror is stellite or polished steel and is placed at a 45-degree angle to the chamber (Fig. 3, A, B). The light source is placed directly over the cell containing the material to be observed. When the rotor is turning fast enough to prevent flickering, one obtains through the microscope an almost perfect image of the material being centrifuged (Fig. 3, A).

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* See also Biscoe, J., Pickels, E. G., and Wycoff, W. G., *Jour. Exp. Med.*, 1936, Vol. 64, p. 39.

As pointed out by Harvey, one of the important problems in high speed centrifuging is to prevent crushing of the material that is centrifuged. This may be obviated by supporting this material in an isotonic medium of graded density so that the material comes to lie in a medium of the same density. Isotonic sucrose, neutralised gum arabic or soluble starch solutions may be used for this purpose. Where large pieces of organs, such as the liver, are centrifuged, the cells next to the sides of the ultracentrifuge, i.e. on the centrifugal side of the liver mass, may be somewhat crushed while serving as a buffer for the rest of the cells which are not affected by the crushing action.

MATERIAL AND TECHNIQUE.

Several species of Fucus may be easily collected in abundance upon the rocks a few feet below the high-tide limits along the shores of Plymouth Sound. *Fucus vesiculosus*, *Fucus platycarpus*, *Fucus serratus*, and *Ascophyllum nodosum* were collected during the months of April, May, and June of 1935 at a point just below the Plymouth laboratory. Observations were made upon all the above-named species of Fucus for comparison, but only those upon *Fucus serratus* are recorded here.

The sexes of *Fucus serratus* can easily be distinguished by cutting and examining the conceptacles. The plants were collected a short time after they had been exposed by the ebb-tide and taken into the laboratory, and the males and females placed in separate dishes. After 6 to 10 hours in the laboratory the fruiting tips were observed to extrude the gametes. Those of the female were extruded in capsules of eight forming an olive-green mound-like mass upon the conceptacle. Those of the male were extruded in capsules containing many sperm (antherozoids) and were of an orange colour. A considerable amount of mucilaginous material is secreted, too, if the plants are kept moist. After tips of the fruiting plants were submerged in sea water, the mucilaginous material and the gametes were washed free ; they then settle readily to the bottom of the dish.

If the female gametes are examined immediately they will be found in groups of eight surrounded by a gelatinous capsule consisting of a definite membrane or membranes, which dissolve after a few minutes in sea water setting the individual eggs free. If the capsules containing the eggs are extruded under unfavourable conditions, such as rapid drying or at too high a temperature, one frequently finds two or more of the eggs fused together giving rise to a capsule of 1 large egg and 6 of normal size (Fig. 5, A). In extreme cases as many as 6 eggs may fuse, giving rise to 1 giant egg and 2 of normal size within the capsule (Fig. 5, B).

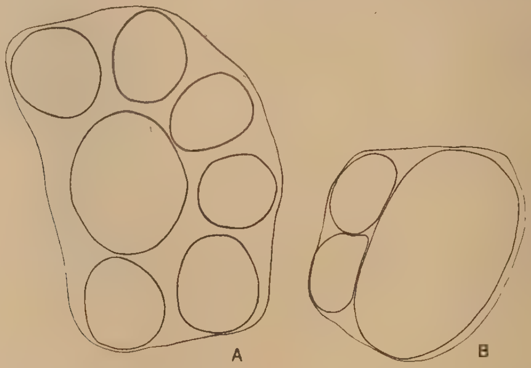

Fig. 5.—Fusion of Fucus eggs inside capsule. A, two eggs fused giving rise to one large egg and six of normal size; B, six eggs fused giving rise to one giant egg and two of normal size.

In addition to observing the eggs alive, they were fixed in Bouin's, Flemming's strong, Flemming's weak, and Champy's solutions. The best results were obtained with Flemming's strong solution made up in sea water. The sections were bleached and stained in Heidenhain's haematoxylin.

The Unfertilized Egg.

Notwithstanding the fact that the centrifuge has proved to be a valuable instrument in the study of many problems of experimental cytology and embryology of animal eggs (see Morgan, 1928, and Wilson, 1925, for reviews of the literature), it has been almost entirely neglected or no results have been obtained in similar types of studies upon plants. Shimamura (1929) centrifuged the egg of *Pinus thunbergii* and reports that "there is no stratification or separation of the contents in the egg cytoplasm." More recently, however, Whitaker (1931) succeeded in stratifying the cytoplasmic materials in the unfertilized eggs of *Fucus vesiculosus*. Various somatic cells of plants have been centrifuged and for a review of the literature on this aspect of the subject the reader is referred to a recent paper by Beams and King (1935).

For a detailed description of the normal cytology of fertilization and of the early cleavages in Fucus the reader is referred to the excellent works of Farmer (1896), Farmer and Williams (1898), Strasburger (1897), Yamanouchi (1909), Oltmann (1922), and Walker (1930).

The normal unfertilized eggs of *Fucus serratus* vary considerably in size (60–90 μ) and possess an alveolar or foam-like type of cytoplasm in which is embedded a well-defined nucleus (Pl. II, Fig. 1). Irregularly distributed throughout the cytoplasm are many chromatophores, fat-bodies and certain other granules of undetermined character. Farmer and Williams have described the chromatophores as located at the surfaces of the foam cavities with their long axes directed away from the nucleus. A cell membrane encloses the cytoplasm and the eggs have been described by some investigators as undergoing amoeboid movement. When the unfertilized egg is centrifuged its components become stratified into three distinct layers from the centrifugal to the centripetal pole as follows (Pl. II, Fig. 2): (1) A layer of very dense alveolar-like clear cytoplasm constituting over two-thirds of the total volume of the egg; (2) a layer of green chromatophores; and (3) a layer of fat in the form of globules or vacuoles at the centripetal pole. The nucleus takes up a position between the chromatophores and fatty globules. Sometimes the eggs become greatly elongated in the direction of the centrifugal force and the fatty layer and part

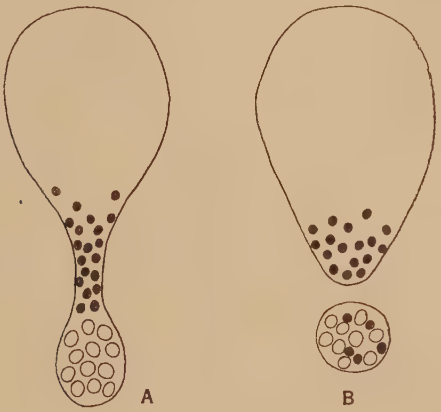

Fig. 6.—Ultracentrifuged unfertilized eggs. A, egg greatly elongated in the direction of the centrifugal force; fat globules and some of the chromatophores fragmenting from the egg. B, later stage of A.

of the chromatophores may be completely removed from the egg (Figs. 6, A, B; Pl. II, Fig. 3). The eggs are very dense as compared to sea-urchin eggs and it was difficult to find a medium of the same density in which they could be suspended while centrifuging without causing a marked osmotic effect. I employed gum arabic and a sucrose solution made up in sea-water, but even then I was not successful in getting a solution of the same specific gravity as the eggs.

The Fertilized Egg.

In about 10 to 15 minutes after fertilization of the eggs of Fucus a distinct cell wall is formed around them which prevents a marked distortion of the eggs during centrifuging. When a fertilized egg with a cell wall is centrifuged in sea-water at 150,000 times gravity a sharp stratification of its protoplasmic components takes place (Pl. II, Fig. 4). Here, as in the unfertilized egg, three distinct zones are present in the order of their decreasing specific gravity as follows: (1) a layer of dense alveolar

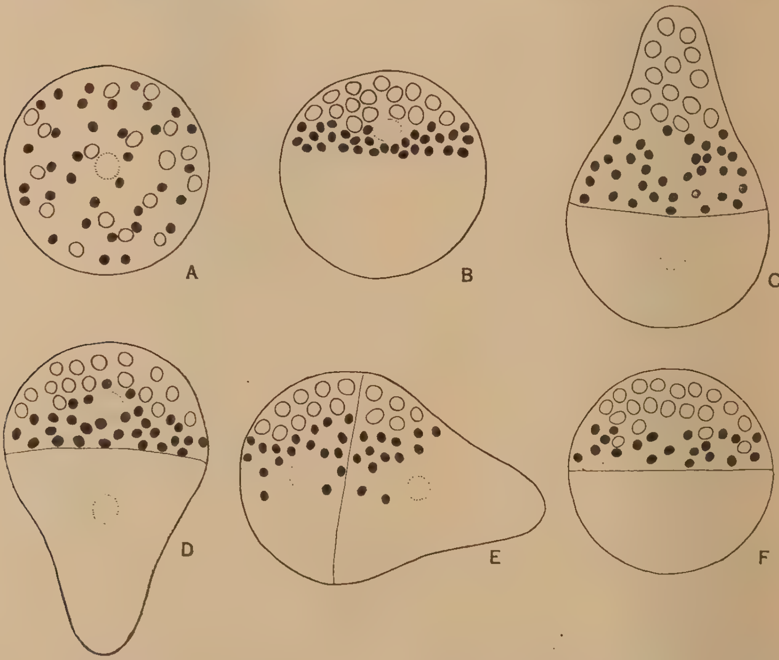

Fig. 7.—A, normal egg; B, stratified egg; C–E, eggs showing appearance of rhizoid protuberances, first cleavage planes and their relations to the planes of the stratified materials. F, egg cleaved without forming rhizoid rudiment.

cytoplasm; (2) a layer of chromatophores and bodies which I have tentatively interpreted as mitochondria; and (3) a layer of fat globules which are readily blackened by osmic acid. The nucleus lies just centripetal to the layer of chromatophores. The egg illustrated in Plate II, Figure 4, was not fixed until one half-hour after it had been centrifuged and shows the initial stages of the migration of the nucleus back to the centre of the egg, its usual position. Conklin (1917) has attributed this phenomenon to the activity of the "spongioplasm." The writer is inclined to believe that the factors involved in the redistribution of the stratified materials are more complex than assumed by Conklin. This point will be further discussed in a forthcoming paper dealing with the effects of centrifuging the eggs of *Ascaris suum*. Small granular bodies are found in the fixed preparations that are readily stratified by ultracentrifuging into a position between the chromatophores and fat globules. I am inclined to interpret them as mitochondria; however, they are obviously in need of further investigation. In Plate II, Figure 5, is depicted a cell fixed 6 hours after centrifuging. It will be observed that the nucleus has returned almost to its usual position within the cell, carrying with it numerous chromatophores and fat globules. However, less frequently, following strong centrifuging cells may be found where only the nucleus migrates to the centre of the egg where cleavage takes place and all or most of the chromatophores and fat globules remain stratified (Fig. 7, C–F;

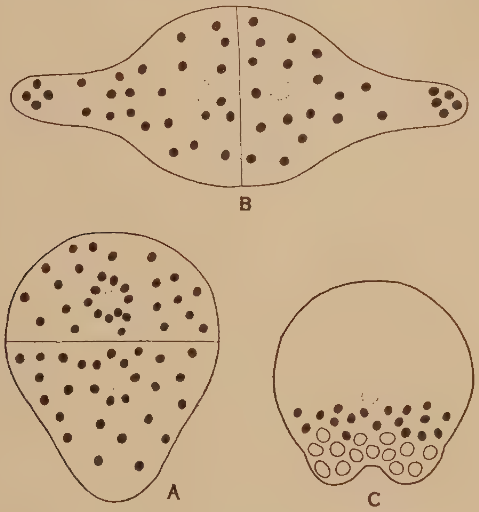

Fig. 8.—A, normal egg; B, bipolar uncentrifuged egg; C, ultracentrifuged egg with two rhizoid protuberances.

Pl. II, Figs. 6–7). In no case was I ever successful in fragmenting the fertilized eggs of Fucus as has been done with the eggs of certain sea-urchins.

As previously pointed out the unfertilized and the fertilized eggs of Fucus for the first 6 to 8 hours after fertilization are unlike many animal eggs, for example, the frog's egg, in that they show no indication of polarity. I have attempted to show diagrammatically (Fig. 7) how the various materials may be stratified in relation to the appearance of the rhizoid protuberance and of the first cleavage plane. Figures 7, A and B, show the typical appearance of the fertilized egg before and after centrifuging, respectively. It will be observed by an examination of Figure 7 that the appearance of the rhizoid protuberance and of the first cleavage plane seems to be irrespective of the plane of the stratified materials. For instance, in Figure 7, C, the rhizoid protuberance appeared at the centripetal pole of the stratified egg and the first cleavage plane occurred parallel to the stratified material separating all of the chromatophores and fat globules into the daughter cell possessing the rhizoid protuberance. However, in Figure 7, D, the rhizoid protuberance has appeared at the centrifugal pole of the egg, and the first cleavage plane, as in the above case, occurred at right angles to the stratified materials dividing the egg so that the daughter cell possessing the rhizoid rudiment is composed chiefly of alveolar cytoplasm and is free of chromatophores and fat globules. In Figure 7, E, the rhizoid protuberance has occurred laterally and the first cleavage plane at right angles to the stratified materials. In still other cases eggs are found which do not give rise to rhizoid rudiments, yet cleavage may take place as indicated (Fig. 7, F).

In some of the control eggs, as well as in the centrifuged material, I have observed certain rather interesting abnormalities. In Figures 8 B and C are shown cells with a dual polarity. Whitaker (1931) has likewise described similar abnormalities in *Fucus vesiculosus*. Although the complete history of these two cells is unknown it seems probable that their dual polarity is due to a fusion of 2 eggs, each of which retained its original polarity. Eggs with as many as 4 nuclei have been found but it is not known whether this is due to a fusion of 4 eggs, polyspermy, or to a division of the nucleus without division of the cytoplasm (Pl. II, Fig. 8).

DISCUSSION.

It has been demonstrated in this paper that the visible inclusions in the eggs of *Fucus serratus* may be shifted and stratified in the order of their relative specific gravity without affecting the normal development or apparently modifying the original polarity, i.e. the original axis of the egg. Neither do the stratified materials seem to play a role as organ-forming substances. In this respect the *Fucus serratus* egg differs from the somatic tissue of another alga, *Griffithsia bornetiana*, recently investigated by Schechter (1934). Schechter found that if tufts of the alga were centrifuged at 150 times gravity for 24 hours or longer, normal shoots appear from the cells at a point where the heavier substances, in this case the chromatophores, have concentrated. In this way reversal of polarity may be produced anywhere along the plant axis. He suggests, however, that the centrifuged substances (inclusions) are not directly determinative of the polarity, but act as stimuli.

The question then follows in what structure or structures of the cells does the polarity reside. This is an old question among students of embryology and one that has never been satisfactorily answered. Lillie (1909), from his work on centrifuged Chaetopterus eggs, concludes that "polarity is a property of the ground substance of the protoplasm" which cannot be disturbed by ordinary centrifuging because it is assumed to be of molecular organization. Conklin (1917, 1924) holds that polarity inheres in the "viscid spongioplasm" which forms a peripheral layer around the egg and a continuous framework throughout the cell that is connected to the nucleus. It is this structure which, he holds, is responsible for the return of the nucleus and other inclusions or components to their usual position within the cell after artificial displacement by centrifuging. The yolk, oil, water, and pigment granules are thought to lie in the meshes of the "spongioplasm." As regards the effect of centrifuging upon the "spongioplasm" Conklin states: " . . . at the same time the strands of the framework may be stretched or bent, but unless the centrifuging is strong enough to kill the egg, this substance is not stratified with the other cell contents."

If one assumes that the "ground substance" of Lillie and the "spongioplasm" of Conklin are molecular, a condition that now applies to protoplasm generally, it might be possible, in view of the recent work of Svedberg (1928), to produce a stratification within the protoplasm of its colloidal components. In this connexion Taylor (1931) has recently raised the question, "But to what extent the living ground substance would endure the rigours of such enormous forces (10,000 to 100,000 times gravity) and remain living is extremely problematical."

It is clear from this work on Fucus that centrifugal force of 150,000 times gravity for 30 minutes does not kill the eggs. But to what extent the "spongioplasm" has been affected by such enormous forces one is unable to state. However, Beams and King (1936) have recently subjected the eggs of *Ascaris suum* to a centrifugal force in excess of 400,000 times gravity for one hour without killing them. This is a force equal to the maximum employed by Svedberg to produce sedimentation of colloids. Ascaris eggs have also been subjected to 150,000 times gravity for 10 days; they not only remain living but undergo cleavage in the ultracentrifuge. It has not yet been determined whether or not a stratification of the colloidal cytoplasmic components has taken place, but if such does take place, it is of particular interest, for then the normal spatial relationship of the separate elements cannot be of vital importance for the maintenance of life. However, if, as we are inclined to believe, little or no separation or stratification of the components has taken place in this material, they must be held together in a firmer way than those in the colloidal systems examined by Svedberg. In other words, the conditions present in this living colloidal system (protoplasm) seem to be different from those in non-living ones.

It would seem that the killing of cells by the present methods of centrifuging is usually due to mechanical distortion or disruption (prevented in the fertilized Fucus egg by a very resistant cell wall and in Ascaris eggs by a shell) rather than to a disturbance of the spatial relationship of their molecular parts.

In Fucus it has been demonstrated by Farmer and Williams (1898), Hurd (1920), Whitaker (1931), and others that light may alter the polarity of the developing spore. They found, and I have also observed, that the rhizoid protuberance always appears on the side of the egg opposite the light (i.e. the shaded side). Hurd further observed that the shorter rays at the blue end of the spectrum were the most effective in determining the polarity. She suggests that this effect may be due to a more rapid oxidation of the egg on the side exposed to the light, setting up a metabolic gradient which is responsible for the polarity. Hurd also found that when eggs were placed in groups very close to one another, each develops a polarity in such a way that its apical point faces toward the group. To this phenomenon, which is even more influential in determining polarity than light, she has given the name of "group orientation effect." Whitaker has shown that even unfertilized eggs of another species may control the polarity in the "group effect." The direct effect, he concludes, cannot be due to any agency depending upon nuclear or cell division.

Lund (1923) has found by passing an electric current through sea water containing eggs of *Fucus inflatus*, that they will all become polarized with the rhizoid protuberance toward the positive pole. This is interesting in view of the findings of McClendon (1910) that the chromatin in the nucleus of the onion root tip moves to the positive pole when exposed to an electric field. However, since Lund did not examine the eggs cytologically it is unknown whether or not the electric current directly affected the mitotic spindle.

It is evident that in many of the eggs like those in Figure 7, all of the chromatophores are segregated into one of the daughter cells at the first cleavage. However, as the spore grows, new chromatophores arise in those cells derived from the chromatophore-free blastomere. Although I do not want to urge the view too strongly, it seems probable that the new chromatophores may arise *de novo* in the cell, perhaps by the activity of certain of the cytoplasmic components.

A few preparations were made by the Kolatchev method in an effort to demonstrate the osmiophilic platelets, but they were unsuccessful. The whole problem of the nature of the mitochondria and the osmiophilic platelets and their relationships to the other cell inclusions of the Fucus egg is badly in need of further investigation.

It has been the author's experience that many of the methods designed to be used on the tissues of fresh-water animals and plants do not always work so successfully upon the tissues of marine animals. It is also a fact of experience that many of the well-known methods fix tissues and cells of marine animals better if they are dissolved in sea water instead of the usual method of using distilled water. In general, a distinct need is felt for a modification of many of our cytological fixatives in order that they will preserve more successfully the cells of marine animals.

SUMMARY.

1. An air turbine ultracentrifuge suitable for biological work and capable of developing a centrifugal force from 10,000 to 500,000 times gravity has been described. Advantages of the ultracentrifuge are: (1) The temperature does not vary in the centrifuge chamber over 2 or 3 degrees from that of the atmosphere; this is not sufficient to be an important factor in general biological work. (2) The cost of constructing the apparatus is very low in comparison with that of other high speed centrifuges.

2. A modification of the air turbine ultracentrifuge in which the turbine rotor drives a second rotor, in this case the centrifuge rotor which spins in a vacuum, has been described. Here the centrifuge chamber is thermally insulated which is an important item in preventing troublesome convection currents from arising in the centrifuged material where such special problems as the rate of molecular sedimentation are being observed. Forces in excess of one million times gravity can easily be obtained by such an apparatus.

3. A microscope ultracentrifuge in which the biological materials may be observed while centrifuging at high speeds (10,000 to 200,000 times gravity) has been illustrated.

4. The stratification in *Fucus serratus* eggs of the visible inclusions in the order of their relative specific gravity by means of the ultracentrifuge has been described. After centrifuging fertilized *Fucus serratus* eggs at 150,000 times gravity for one half-hour they apparently develop normally.

5. The polarity in centrifuged Fucus eggs as determined by the appearance of the rhizoid protuberance and of the first cleavage plane is unaffected by a stratification of the visible inclusions.

6. The fusion of as many as six unfertilized eggs has been observed.

7. Normal and centrifuged bipolar eggs, i.e. with two rhizoid protuberances, have been found. This condition is probably due to the fusion of two eggs each of which has retained its original polarity.

Acknowledgement.

The author is greatly indebted to Dr. E. J. Allen, F.R.S., for kindly placing at his disposal during the summer of 1935 all the facilities of the Plymouth Laboratory. To Dr. W. R. G. Atkins, F.R.S., and other members of the staff of the Plymouth Laboratory the author is also indebted for much help and advice regarding the collecting and handling of Fucus. I am also very grateful to Professor J. W. Beams and Dr. E. G. Pickels for constructing the ultracentrifuges for me. Finally, I wish to thank Professors R. L. King and J. Brontë Gatenby for kindly reading the manuscript.

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EXPLANATION OF PLATE II.

All drawings were made from sections at an approximate magnification of 2,000 times. Centrifugal ends of the cells, except Figure 1, are directed toward the bottom of the plate.

Fig. 1.—Normal unfertilized egg.

Fig. 2.—Ultracentrifuged unfertilized egg showing stratification of the visible materials.

Fig. 3.—As in 2, but elongated in the direction of the centrifugal force.

Fig. 4.—Fertilized ultracentrifuged egg showing stratification of materials.

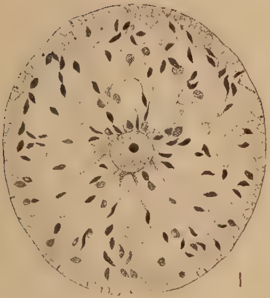
Fig. 5.—As in 4. Nucleus and inclusions shown in the process of returning to their usual position within the egg.

Fig. 6.—Spore derived from egg in which most of the inclusions had been segregated into the daughter cell opposite the one possessing the rhizoid protuberance at the first cleavage.

Fig. 7.—Spore derived from egg in which most of the inclusions had been segregated into the daughter cell possessing the rhizoid protuberance at the first cleavage.

Fig. 8.—Uncleaved ultracentrifuged egg with four nuclei.

PLATE II.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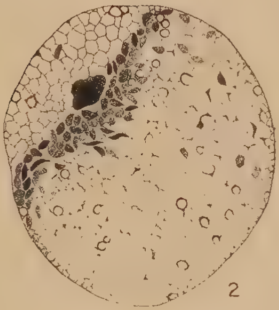
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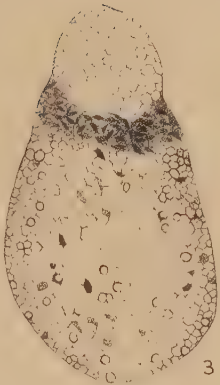
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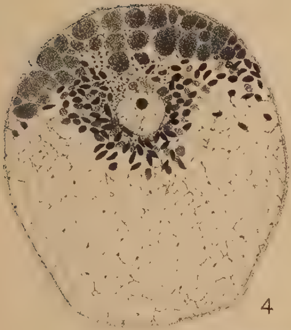
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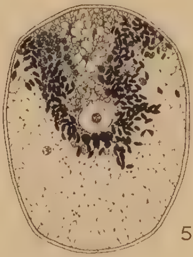
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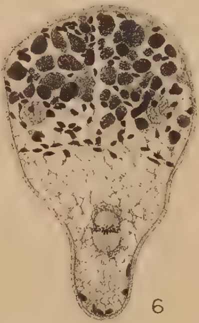
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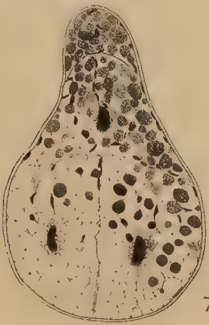
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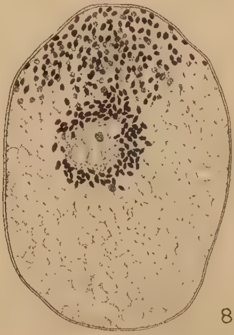
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Del., Gladys Larsen

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To face page 588.

A Review of the Amphipod Genus *Corophium*, with Notes on the British Species.

By

G. I. Crawford, M.A.,

Assistant-Keeper at the British Museum (Natural History): late Student Probationer at the Plymouth Laboratory.

With 4 Figures in the Text.

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INTRODUCTION.

During 1934–5 I collected in Plymouth Sound and neighbouring waters seven species of the genus Corophium of which two were undescribed. I also collected one other species, and had sent to me two other species (one new) from other localities in South England. A list of these ten species, with the single other species known from Britain, is given in Appendix II, and their British distribution summarized.

In the course of identifying them I examined 23 of the 32 species of Corophium, and saw all the literature to which I could find references.

The first part of this paper consists of a general account of the morphology and ecology of the genus and a key by which it can be divided into three sections. This part is introductory to the second part, which contains a review of those species which I consider valid. In this review the name of each species is followed by a complete bibliography, only those references being omitted which have already been listed by Stebbing (1906): if a number of references have been made to a species, that which contains the best description or figures is placed in square brackets above the others, and immediately below the name of the species. An account of distribution follows the bibliography, and is followed for many species by notes on ecology and identification.

Description and figures are given of the three new species: and keys have been made to two of the sections (13 spp.). Holotypes and paratypes of new species are in the British Museum (Natural History).

GENERAL ACCOUNT.

HISTORICAL.

The genus *Corophium* was established by Latreille in 1806, to include the single species *C. longicorne* (which had previously been described as *Oniscus volutator* Pallas).

The best general account is that of Stebbing (1906), who defines the genus, and gives a key to 12 species, with descriptions and full bibliography. Bradley (1908) gives a key to 15 species (not 16 as appears, for *C. cylindricum* and *C. acherusicum* are synonymous), and excellent figures and descriptions of *C. salmonis* and *C. spinicorne*. He does not describe the other species, or list bibliography, and his key is inferior to Stebbing's. Both these accounts need revision, since the number of species has since been doubled.

Many fauna lists of separate areas have been published. The following are the most important.

Della Valle (1893), 3 spp., Naples.
Sars (1894), 4 spp., Norway.
Sars (1895), 6 spp., and (1896), 1 sp., Caspian Sea.
Chevreux (1908), 3 spp., Bône, Algeria.
Chevreux and Fage (1925), 6 spp., France.
Stephensen (1929), 5 spp., Nord und Ost-See.
Shoemaker (1934 *a*), 9 spp., E. coast of N. America.
Shoemaker (1934 *b*), 2 spp., W. coast of N. America.

The bionomics of *C. volutator* are described by Hart (1930); and those of *C. insidiosum* n.sp. by Ussing (1924) under the name of *C. bonelli*.

ECOLOGY.

As far as is known all species form tubes of mud or muddy sand, either in the substratum or upon ascidians, sponges, etc. These two habitats are each frequented by about half the species of Section A, as defined below, but with the exception of *C. crassicorne* in Section B no species of the other sections is known to burrow. The tubes of *C. volutator* and *C. insidiosum* are described respectively by Hart (1930) and Ussing (1924).

The species of this genus are found in shallow water, and frequently between tidemarks. They are characteristic, especially the species which build tubes on sessile objects, of harbours and estuaries, where there is much silt for the forming of tubes. Many are able to endure slight diminutions of salinity in the surrounding water, and a few species live in fresh, or nearly fresh, water. *C. rioplatense* was described from specimens found in fresh water in the Rio de la Plata, *C. spinicorne* has been found in the San Francisco water supply, and *C. curvispinum* var. *devium* is common in the freshwater reaches of many European rivers.

The feeding of *C. volutator* is described by Hart (1930). This species is principally a selective deposit feeder, and also consumes a small proportion of suspended particles. The form of the limbs chiefly used in feeding—the maxillipedes and the two pairs of gnathopods—is so constant throughout the genus that it is probable that other species differ only in the proportions of the food-supply drawn from these two sources.

In the British species (except for *C. bonelli*) both sexes are usually present in collections, though the female is usually rather commoner than the male: and this appears, from the literature and specimens that I have seen, to be so with most species of the genus. *C. bonelli*, however, is almost certainly parthenogenetic—a condition rarely found elsewhere in the Amphipoda. The evidence on which I base this conclusion is summarized in the account of that species.

Some species, e.g. *C. acutum*, are almost world-wide in distribution. Species which build tubes on sessile objects are clearly likely to be carried by shipping, and *C. acherusicum* has been collected off a ship's bottom at Sheerness.

MORPHOLOGY.

A full definition of the genus is given by Stebbing (1906). The features most characteristic of the genus are the second antennae, the mandibular palp (which is 2-jointed), and both pairs of gnathopods. In the male antenna II, segment 4 is normally stout and terminates with a single or complex tooth: this segment may also bear spines. In many species of Section A this segment is similar in the female to that of the male: in others, and in almost all species of Sections B and C, this segment in the female bears no teeth, but only spines, the arrangement of which is specifically distinctive. These features are well shown in the drawings of Sars (1894), whose general account of the genus on pages 612–3 is also excellent.

The genus may be divided into three sections on the characters of the urosome: no species are known with intermediate characters.

Section A:	segments of urosome separate (19 spp.—10 accepted by Stebbing in 1906).
Section B:	segments of urosome fused; uropods I and II inserted in notches in the lateral margins of the urosome (8 spp.—2 accepted by Stebbing).
Section C:	segments of urosome fused; uropods I and II attached ventrally; lateral margins of urosome without notches (5 spp.—none known to Stebbing).

The fusion of the segments of the urosome has proceeded further in Section C than in Section B, and therefore the species of Section C seem to have developed most, and those of Section A least, from their hypothetical common ancestor. Fusion of the urosome segments is not common in the Amphipoda. The characters of these sections are further considered in the appropriate place in the review of species.

Certain species have frequently been confused with each other, especially *C. crassicorne*, *C. bonelli*, *C. insidiosum*, and *C. acherusicum*, and to a less extent *C. acutum* and *C. lacustre*. This is due to incomplete knowledge of distribution and of literature, and even more to attention wrongly paid to characters which are not specific.

For identification, adult specimens (ovigerous ♀♀ and ♂♂ therewith) of both sexes should be examined, and the following features observed: form of rostrum, eye-lobes, eyes; antenna I, form of basal segment and arrangement on it of outgrowths, spines and setae, ratio of lengths of first three segments, number of segments in flagellum; antenna II, segments 4 and 5, form of segment and arrangement of spines, teeth or processes, and density and length of setae; gnathopod I, form of palm, spines on it, and subsidiary teeth on dactyl; gnathopod II, subsidiary teeth on dactyl; pereiopods 5 and 6, spines on carpus; pereiopod 7, form of basal segment and ratio of its length to that of propod; urosome, segments separate or fused, and shape of lateral margin; uropods I and II, spines on peduncle and rami; uropod III, form of ramus; telson, form.

Of these the characters of the urosome; of antenna I, segment 1; and of antenna II, segments 4 and 5, are the most useful. The gnathopods, though very characteristic of the genus, and not similar in form in every species, are usually very similar in related species. The mouth-parts are very uniform, as far as is known.

The characters of the antennae change with age, and even in adults some variation occurs. Variation in *C. curvispinum* is described by Wundsch (1915), in *C. salmonis* and *C. spinicorne* by Bradley (1908), and in *C. volutator* by Hart (1930). In this paper I have described variation in *C. arenarium*, *C. bonelli*, *C. insidiosum*, *C. acherusicum*, and *C. sextoni*. In these, and in *C. crassicorne*, the antennae of juveniles are shorter in relation to the body; the segments are stouter, and bear more spines in the male and less in the female. The adult male in these five species bears only a few small spines on the antennae. Outgrowths on antenna I, segment 1, and antenna II, segment 5, which are characteristic of the males of some species, are only present in full-grown specimens: the same is true of the very long rostrum of the adult male of *C. aculeatum*, *C. insidiosum*, and *C. uenoi*.

The number of segments on the flagellum of antenna I, of subsidiary teeth on the dactyl of gnathopod II, and of spines on the uropods increases with age.

Measurements of length given in this paper are from rostrum to telson.

REVIEW OF SPECIES.

SECTION A.

This section contains 19 species, of which one is here described as new. I have examined 13 of these, the remaining six being *C. spinulosum* Sars, *C. maeoticum* Sowinsky, *C. salmonis* Stimpson, *C. spinicorne* Stimpson, *C. rotundirostre* Stephensen, and *C. rioplatense* Giambagi.

I have not made a key to the section, since the specific differences do not lend themselves to the necessary terse description, and adequate figures have been published of every species. Stebbing (1906) included a key to 10 species with full synonymy and description. Bradley (1908) gave a key to 13 species, with the synonymy, descriptions and figures of *C. salmonis* and *C. spinicorne* only. His key is not, however, of great use as he relied on characters common to both sexes and these are not well known or distinctive.

In about half the species segment 4 of antenna II in the female differs from that of the male only in being less strongly developed. Several are of large size (8–12 mm.) compared with those of Sections B and C. *C. rioplatense*, *C. curvispinum* var. *devium*, and *C. spinicorne* have been found in fresh water; and many other species inhabit water of low salinity. The majority of species for which information is available are burrowers. Most are restricted in distribution in comparison with those of Sections B and C.

The type species of the genus is *C. volutator* Pallas, which is recorded from Europe (including the Sea of Azov) and the Eastern coast of North America. It bears much resemblance to *C. arenarium* from England and North France, a species here described as new; to *C. salmonis* and *C. spinicorne* from California; to *C. maeoticum* from the Sea of Azov; and to *C. nobile*, *chelicorne*, *spinulosum*, *robustum*, *mucronatum*, *curvispinum*, and *monodon* from the Caspian Sea and neighbouring waters. In all these species (except *C. arenarium*) antenna II, segment 4, differs little in the two sexes, and in many of the species from the Caspian Sea and Sea of Azov this segment bears a complex armature of terminal teeth. All are at least of moderate size and many are large (4–12 mm.).

C. aculeatum, *C. annulatum*, and *C. runcicorne* from the Mediterranean, with *C. affine* from the North Sea and Arctic seas, form a natural group of rather small burrowing forms (1·5–5 mm.) of slender build, and with uropod III linear in shape. The only known specimens of *C. rotundirostre* (also from the Mediterranean) have antenna II missing; it is not, therefore, known if this species resembles the other four in having antenna II, segment 4, unlike in the sexes. In other features it is rather similar to *C. annulatum*, though much larger.

C. triaenonyx from Ceylon and *C. rioplatense* from fresh water in the Rio de la Plata are two non-burrowing species of moderate size (3–4 mm.). The form of antenna II, segment 4, in the female distinguishes them from each other and from other groups. Probably a better knowledge of surrounding regions would reveal species related to them.

1. COROPHIUM VOLUTATOR (Pallas).

[Sars, G. O., 1894, p. 614, pl. 219 as *C. grossipes*.]

1816, *C. v.*, Leach, Encyc. Brit., p. 401. 1821, *C. longicorne*, d'Orbigny, J. Phys. Chim. d'Hist Nat. Arts, 93, pp. 194–200. 1825, "*Corophie à longues cornes*," Desmarest, Consid. Gen. Sur. Classe. Crust., p. 270. 1829, "*La Corophie longues-cornes*," Latreille, in Cuvier's Règne Animal, 4, p. 123. 1840, *C. l.*, Milne-Edwards, H., Hist. Nat. Crust., 3, pp. 66–7. 1857, *C. v.*, White, Pop. Hist. Brit. Crust. 1859, *C. l.*, Bruzelius, Svensk. Ak. Handl., N.S., 3, No. 1, p. 14. 1862, *C. l.* (part—the specimens found with *Jassa falcata* are probably some other sp.), Bate, Cat. Brit. Mus., p. 280, pl. 47, f. 4. 1863, *C. l.*, Bate, Brit. Sess. Eyed Crust., 1, p. 493. 1869, *C. l.*, Brady. Nat. Hist. Trans. Newcastle, 3, p. 120. 1873, *C. l.*, Parfitt, Trans. Devon. Ass. F. Devon, 9, p. 13. 1874, *C. l.*, and ? *C. bonelli*, Bos, Biol. Crust. Hedriopth. Ned., pp. 28, 52. 1879, *C. l.*, Hoek, Tijdschr. Ned. dierk. Ver., 4, p. 115. 1884, *C. l.*, Blanc, Nova Acta. K. Leop. Carol., 47, No. 2, pp. 82–85, f. 102–114. 1885, *C. l.*, Gadeau de Kerville, Estuaire de la Seine, 2, p. 181, Havre. 1886, *C. grossipes*, Herdman, 1st Rep. Liverp. Bay. 1888, *C. v.*, Robertson, Trans. Nat. Hist. Soc. Glasg., 2, p. 61. 1889, *C. g.*, Hoek, Tijdschr. Ned. Dierk. Ver., Ser. 2, 2, p. 230, pl. 8, f. 4–8. 1898, *C. v.*, Sowinski, Bull. Acad. Sci. St. Pétersb., Ser. 5, 8, p. 361. 1901, *C. g.*, Elliott, F. Fl. and Geol. Clyde Area, p. 342. 1901, 1903, *C. g.*, Allen and Todd, J. Mar. Biol. Assoc., 6, pp. 151, 295. 1906, *C. g.*, Scott, Proc. R. Phys. Soc. Edinb., 16, pp. 172, 379: 1906, *C. l.*, Sinel, Trans. Soc. Nat. Sci. Guernsey, p. 212. ? 1906, *C. l.*, Sinel, Outline Nat. Hist. our Shores, p. 119. 1906, *C. v.*, Norman and Scott, Crust. Devon and Cornwall, p. 95. 1906, *C. v.*, Stebbing, Das Tierreich, 21 (1), p. 686. 1907, *C. g.*, Colgan, Irish. Nat., 16, p. 181. 1907, *C. g.* (part), Gurney, Trans. Norfolk. Norw. Nat. Soc., pp. 414, 417, 421, 427 (part), 435 (part), table II (part) (see also *C. lacustre*). 1907, *C. v.* Norman, Ann. Mag. Nat. Hist., Ser. 7, 20. 1907, *C. l.*, Patterson, Wild Life on a Norfolk Estuary, p. 223. 1908, *C. v.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1911, *C. v.*, Chevreux, Mem. Soc. Zool. Fr., p. 270. 1914, *C. v.*, Stubbs, Zoologist (4), 18, p. 54. 1918, *C. g.*, Hellen, Medd. Soc. Fauna Fl. Fennica, 45, p. 136. 1920, *C. v.*, Mercier, C. R. Acad. Sci., 170, p. 410. 1922, *C. l.*, Flattely and Walton, Biology of the Seashore (London), p. 167. 1922, *C. g.*, Tesch, Fl. and Fauna Zuiderzee, p. 335, f. 7. 1923, *C. v.*, Schlienz, Arch. Hydrobiol. Plankt., 14, p. 429. 1925, *C. v.*, Chevreux and Fage, F. de France, 9, p. 364, f. 372. 1926, *C. v.*, Legueux, Bull. Soc. Linn. Normandie, Ser. 7, 8, pp. 93–4. 1926, *C. v.*, Poisson and Legueux, Bull. Soc. Zool. Fr., p. 322. 1926, *C. v.*, Ranson, C. R. Socs. Sav. Paris and Dep., p. 413, f. 1. 1927, *C. v.*, Stephensen, Vidensk. Medd. Naturh. Foren., 84, p. 139. 1929, *C. g.*, Gurney, Trans. Norfolk. Norw. Nat. Soc., 12, p. 550. 1929, *C. g.*, Percival, J. Mar. Biol. Assoc., 16, p. 81. 1929, *C. v.*, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Crustacea Amphipoda, pp. 1–40. 1929, *C. v.*, Stephensen, Die Tierwelt der Nord- und Ostsee, 14, x. f., p. 168–9, f. 40. 1930, *C. v.*, Hart, Trans. Norfolk. Norw. Nat. Soc., 13, p. 32–3. 1930, *C. v.*, Hart, J. Mar. Biol. Assoc., 16, p. 761, f. 1–4. 1930, *Corophium*, Lambert, Proc. Zool. Soc. Lond., p. 801. 1930, *C. v.*, Trusheim, Senckenbergiana, 12, p. 254, f. 1–3. 1931, *C. v.*, Elmhirst, Proc. Roy. Soc. Edinb., 51, No. 21, p. 171. 1931, *C. v.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, p. 168. 1932, *C. v.*, Elmhirst, Glasg. Nat., x, No. 2, pp. 56–62. 1933, *C. v.*, Nicol, Dove. Mar. Lab. Rep., Ser. 3, No. 1, p. 51. 1934, *C. v.*, Serventy, Norf. Norw. Nat. Soc., Scolt Head Island, pp. 204–5. 1934, *C. v.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 23–4. 1935, *C. v.*, Nicol, J. Mar. Biol. Assoc., 20, p. 203.

DISTRIBUTION. Europe: Ireland, Scotland, England, Wales; W. Norway, the Baltic; European coasts to the Adriatic; Sea of Azov. America: Maine (in stomach of a duck); Bay of Fundy.

C. volutator is the type species of the genus, and is by far the most familiar and frequently collected. Its ecology is treated by Hart (1930).

It is frequently very abundant, forming tubes intertidally in the mud of estuarine mud-flats, salt-marsh pools, and brackish ditches. In some of the streams running into the Tamar it lives in almost fresh water associated with a number of insect larvae, e.g. *Calopteryx splendens* (Dragonfly). In many of its localities, however, the water is nearly of full salinity.

1a. COROPHIUM VOLUTATOR form ORIENTALIS Schellenberg.

1928, *C. v.* f. *o.*, Schellenberg, A., Trans. Zool. Soc. Lond., 22, p. 673.

DISTRIBUTION. Suez Canal. ? Coast of Cirenaica.

Schellenberg's specimens are in the British Museum (1928.9.5, 321–325). I am unable to distinguish from them some specimens from Cirenaica, collected by Chaworth Musters (1926.10.28, 15–21).

There are two ovigerous females in Schellenberg's material, and these differ only from *C. arenarium* n.sp., described below, in bearing no spines on antenna II, segment 5; these spines are not always present in *C. arenarium*. These females bear two spines on antenna II, segment 4, not a "spine-like tooth." Further collecting will probably show that *C. arenarium* is the same as *C. volutator* form *orientalis*.

A number of the features remarked on by Schellenberg as if they were characteristic of his specimens are also present in *C. volutator*, and in *C. arenarium* from Leigh-on-Sea and Roscoff. These are: the form of the gland-cone, the proportions of gnathopod II, the presence of toothed ridges on the telson (omitted from Sars' figures of *C. volutator*, 1894), and the form of the peduncle of urosome III. Stebbing's small-scale drawing of this segment, to which Schellenberg refers, is misleading and much inferior to that of Sars. The only one of Schellenberg's distinctions

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EXPLANATION OF FIGURE 1.

Corophium arenarium n.sp. × 52.

A–C.—♂ paratype.
  A.—Antenna II.
B, C.—Antenna I, segment 1 from above and from side.
D–I.—♀ holotype.
  D.—Antenna II.
  E.—Antenna I, segment 1 from above.
  F.—Antenna I, peduncle from side.
  G.—Uropod I.
  H.—Uropod II.
  I.—Uropod III.

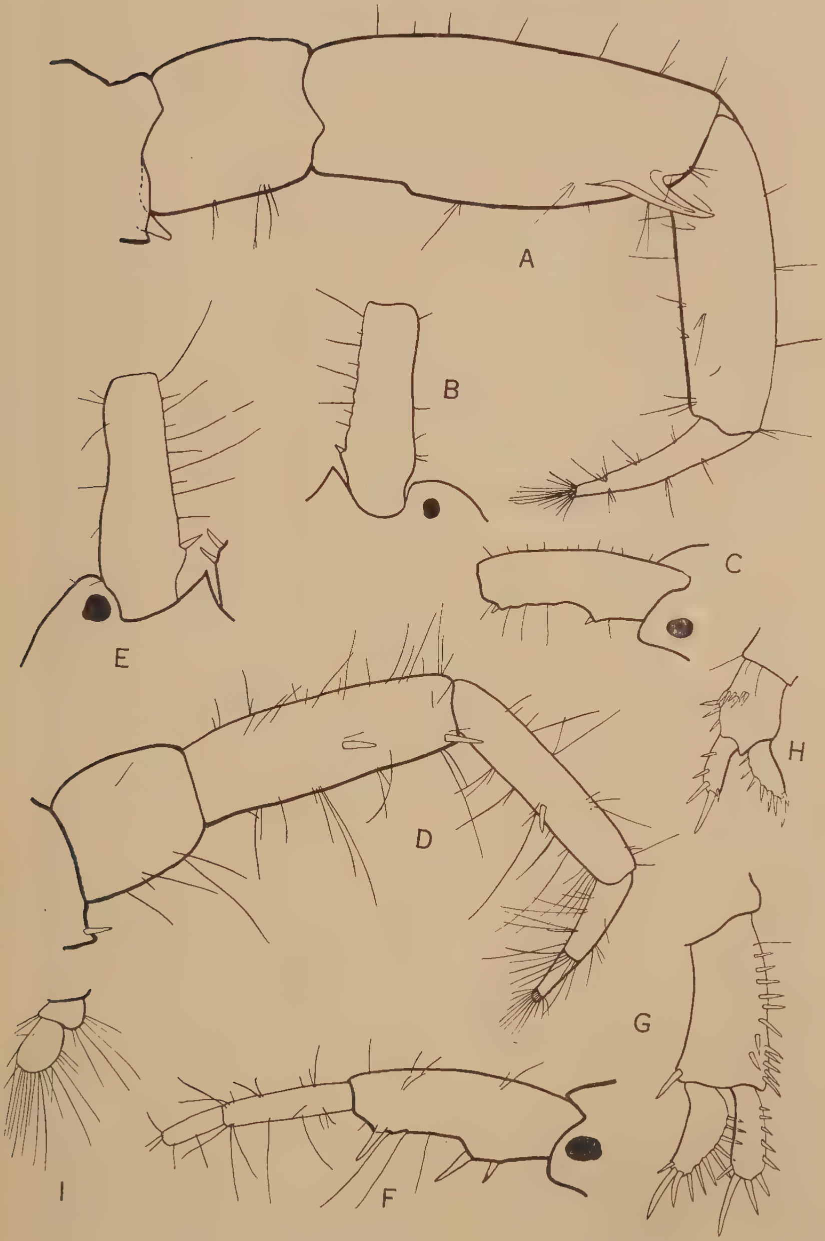

FIG. 1.

which I find valid is that in his specimens the merus of pereiopod 6 bears only simple, as distinct from ciliated, setae. I also note that in both sexes the lower edge of antenna I, segment 1 is strongly convex, so that this segment appears in side view much stouter than in *C. volutator* or *C. arenarium.*

2. Corophium arenarium n.sp.

Figure 1, A–I.

DESCRIPTION OF FEMALE HOLOTYPE (Fig. 1, D–I). Leigh-on-Sea, Essex, 3.viii.30, ovigerous.

Length 6 mm. *Rostrum* in the form of an equilateral triangle. *Eye-lobes* rounded, not reaching to tip of rostrum. *Eyes* rather small.

Antenna I: 30% of total length; segment 1 >2+3, lower edge with 2 spines near the base—the edge between these and the terminal spine concave, bearing 3 setae; inner edge with 1 (left) or 2 (right) spines near base, and several long setae distally; outer edge with a few short setae: segment 2, cylindrical, with several long setae; flagellum, 11-segmented <segments 1+2.

Antenna II: 35% of total length; segment 4, cylindrical, with 2 spines on lower edge, one terminally, and one at about $\frac{2}{3}$ of the way to the distal end; segment 5 bears a single spine at the centre of its lower edge; flagellum, 3-segmented.

Mouth-parts as in *C. volutator*; all the appendages are very similar to those of that species. *Gnathopod I*, palm nearly straight, making rather less than a right angle with the hind margin of the propod: dactyl simple. *Gnathopod II*, dactyl simple. *Pereiopods* 5–6, merus very setose, with front distal corner much produced. *Pereiopod* 7, basal segment oval.

Urosome segments distinct. *Uropod I*, peduncle with 13 spines on outer edge (distally set in a double row), 1 on inner edge; rami with 9–10 spines, of which the distal spines are $>\frac{1}{2}$ the length of the ramus. *Uropod II*, peduncle with 3 spines on the outer edge, and 6 spines continuing this series in a slanting row across the upper surface; inner ramus with 5 spines, outer with 8. *Uropod III*, ramus elongate-ovate, with numerous long setae. *Telson* terminally rounded.

DESCRIPTION OF MALE PARATYPE (Fig. 1, A–C). Leigh-on-Sea, 3.viii.30.

Length 4 mm.

Antenna I: 40% of total length; segment 1 >2+3, lower edge with a small basal and a small terminal spine, between which the edge is crenulate and bears 3 setae; inner edge, with a small basal spine, beyond which it is crenulate and bears several setae (in other males, presumably younger, these crenulations are not present), outer edge with scattered short setae; flagellum, 9-segmented at least, but mutilated distally (10- or 11-segmented in males from Roscoff).

Antenna II: 70% of total length; segment 4 with a single long terminal tooth; segment 5, simple, cylindrical; flagellum obscurely 3-segmented.

Other features as in female.

This specimen is plainly not fully grown. A male from Leigh-on-Sea, collected on June 28th, 1936, measured 5 mm. Antenna I was slightly over 50% of this length, and had 15 segments in the flagellum; antenna II was slightly over 100% of the body-length. The spines on the basal segment of antenna I had disappeared.

IDENTIFICATION AND RELATIONSHIPS. This species is certainly very closely related to *C. volutator*, from which all male and some female specimens can scarcely be distinguished except by their smaller size and different habitat. The notes on variation below suggest that it is only a variety of this species. Until, however, further work has been done on the varieties and growth-changes of *C. volutator* the most satisfactory course is to regard *C. arenarium* as a distinct species. M. Chevais of Paris tells me he hopes shortly to publish a paper on these two species.*

VARIATION. The material originally examined consisted of a few males and ovigerous females from Leigh-on-Sea, Essex, collected by Mr. F. J. Lambert in 1930. In the early spring of 1936 M. Chevais of Paris sent me large collections from Roscoff. Though the females were as large as the type only six were ovigerous (probably it was too early in the year). On June 28th, 1936, Mr. Lambert kindly conducted me to the type locality, where I was able to study the habits of this form and collect numerous specimens, including 28 ovigerous females of 4–6 mm. length.

The majority of these females closely resembled the type; in others antenna II resembled that of *C. volutator* female, bearing a terminal tooth on segment 4, and no spines on segments 4 and 5. The number of specimens belonging to these extreme forms, and intermediates is shown in Table I. The number of segments in the flagellum of antenna I is given as an index of age: it appears that these differences are not due to growth, but are present in specimens of uniform maturity.

In *C. volutator* a terminal spine is often present on antenna II, segment 4, in immature females, but never, in my experience, in ovigerous females. Nor, even in immature specimens, have I seen the other spines on segments 4 and 5 which are frequent in *C. arenarium*.

ECOLOGY. On June 28th, 1936, *C. arenarium* was found burrowing in firm but slightly muddy sand between Ray Gut and the channel running past Leigh Station. Its range extended from about half-tide mark to low water of neap tides. The water which covers these flats at high tide is practically of full North Sea salinity. I understand from M. Chevais that the conditions at the Plage de Madeira, Roscoff, are similar.

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* In "Travaux de la Station biologique de Roscoff."

TABLE I.

Variation of Spines on Antenna II of *C. arenarium.*

	Number of specimens.	Average and extreme number of segments in Ant. I, flag., as an index of age.
Antenna II as in type	17	11·6 (10–13)
Antenna II, 2 spines on segment 4, 0 on segment 5.	4	11·2 (10–12)
Antenna II, Segment 4 with median spine and terminal tooth, no spine on segment 5.	2	12·0 (12)
Antenna II, segment 4 with terminal tooth, no spines on segments 4 or 5 (resembled *C. volutator* ♀).	5	12·6 (11–13)

At Leigh the number of burrows per sq. m. was in the order of 10 to 100. Above each of these was a slight pile of sand, around which radiated furrows of about ¼″ in length, made presumably by the second antennae. Internally the burrows were smooth, and coated with a shining brownish secretion. Many were in the form of a U, with vertical arms of 2″–4″ in length, the other opening being about ½″ from the sand-pile, and not discernible from outside. The animal was generally found about ½″ to ¾″ below the opening with the sand-pile. Some burrows appeared to be straight and to have no second opening.

Several burrows contained two specimens, always, as far as could be told on the spot, a male and a female. Two pairs which I collected separately each consisted of a large male (5 mm.) and a smaller female (4 mm.) with brood pouch lamellae well developed, but not fringed with hairs. I did not record whether large males were ever found alone. During the day's collecting adult females were 3 or 4 times as common as males of comparable size.

In other burrows I found females (never with males) with newly hatched young of about 1 mm. long. These young specimens formed burrows of a few millimetres in length, communicating with that of the parent by minute holes in the smooth lining, usually about ¾″ below the sand-pile. The only female found with young which I later examined under a microscope had brood lamellae fringed with long hairs, but was not bearing eggs.

These few observations can give no more than indications of the habits of the animal. It seems likely that in the burrows containing couples the males were waiting for the females to moult in order to impregnate them then, since these females had no hairs on the brood lamellae, and so could not carry eggs without first moulting. It appears also from the behaviour of the newly hatched young that the burrows are of some permanence. Presumably the young must become independent of the female at latest by the time of her next moult.

Thamdrup (1935) gives a more detailed description of this type of tube, made in sand between tidemarks on the Danish coast (pp. 40, 41, 47, Figs. 12–16), and compares it with the ordinary tube of *C. volutator* (p. 47, Fig. 20), which he also found, but not in the same areas. His observations on the presence of pairs of adults, and of young, in these tubes agree with mine but are more complete. He does not remark on any morphological differences between the inhabitants of these two types of tubes. I have not been able to examine his specimens, but I think that he must have found both species.

3. COROPHIUM NOBILE G. O. Sars.

[Sars, G. O., 1895, p. 292, pl. 20, 21.]

1906, *C. n.*, Stebbing, Das Tierreich, 21 (1), p. 687. 1908, *C. n.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924–5, *C. n.*, Behning, Int. Rev. Hydrobiol., 12, p. 228; 13, p. 46. 1924, *C. n.*, Spandl, S. B. Akad. Wiss. Wien., 133, pp. 476, 500. 1928, *C. n.*, Behning, Binnengewasser, 5, Leben des Wolgas, p. 122.

DISTRIBUTION. Caspian Sea, Black Sea, R. Volga for 232 km. from the mouth.

4. COROPHIUM CHELICORNE G. O. Sars.

[Sars, G. O., 1895, p. 299, pl. 22.]

1906, *C. c.*, Stebbing, Das Tierreich, 21 (1), p. 687. 1908, *C. c.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1924, *C. c.*, Martynov, Russk. Gidrobiol. Zh., p. 210. 1924, *C. c.*, Spandl, S. B. Akad. Wiss. Wien., 133, pp. 476, 500. 1925, *C. c.*, Behning, Int. Rev. Hydrobiol., 12, p. 228, 13, p. 46. 1928, *C. c.*, Behning, Binnengewasser, 5, Leben das Wolgas, p. 122. 1929, *C. c.*, Buchalowa, Zool. Anz., 85, p. 254.

DISTRIBUTION. Caspian Sea, Black Sea, R. Volga for 232 km. from the mouth.

4a. COROPHIUM CHELICORNE G. O. Sars, praenatio FLUVIATILE Martynov.

1924, *C. c.*, prn. f. Martynov, Annu. Mus. Zool. Acad. St. Petersb.

DISTRIBUTION. R. Don.

5. COROPHIUM SPINULOSUM G. O. Sars.

[Sars, G. O., 1896, p. 481, pl. 12, f. 18–25.]

1906, *C. s.*, Stebbing, Das Tierreich, 21 (1), p. 688. 1908, *C. s.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1924, *C. s.*, Spandl, S. B. Akad. Wiss. Wien., pp. 476, 500.

DISTRIBUTION. Caspian Sea.

6. COROPHIUM ROBUSTUM G. O. Sars.

[Sars, G. O., 1895, p. 304 (as *C. robustum*); pl. 23, f. 10–16 (as *C. bidentatum*)].

1896, *C. r.*, Sowinski, Mem. Soc. Nat. Kiew., 15, p. 376. 1906, *C. r.*, Stebbing, Das Tierreich, 21 (1), p. 689. 1908, *C. r.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924, *C. r.*, Spandl, S. B. Akad. Wiss. Wien., pp. 476, 500.

DISTRIBUTION. Caspian Sea, Black Sea.

7. COROPHIUM MUCRONATUM G. O. Sars.

[Sars, G. O., 1895, p. 307, pl. 24, f. 1–7.]

1896, *C. m.*, Sowinsky, Mem. Soc. Kiew., 15, p. 375. 1906, *C. m.*, Stebbing, Das Tierreich, 21 (1), p. 689. 1908, *C. m.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924, *C. m.*, Spandl, S. B. Akad. Wiss. Wien., pp. 476, 500.

DISTRIBUTION. Caspian Sea.

8. COROPHIUM CURVISPINUM G. O. Sars.
8a. C. C. var. DEVIUM Wundsch.
8b. C. C. subsp. SOWINSKYI Martynov.
8c. C. C. prænatio FLUVIATILIS Martynov.

[Sars, G. O., 1895, p. 302, pl. 23, f. 1–9, and Wundsch, H. H., 1915, p. 56, pl. 1–7, f. 1–9.]

1895, *C. c.*, Sars, Bull. Acad. Sci. St. Petersb., Ser. 5, 3, p. 302, pl. 23. 1906, *C. c.*, Stebbing, Das Tierreich, 21 (1), p. 690. 1908, *C. c.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1911, *C. c.*, Beling, Arb. Biol. Dnjeper. Sta. Kiev., 1, p. 114. 1912, *C. c.* v. *d.*, Dershavin, Arb. Ichth. Kasp.-Wolg. Fisch. in Astrachan, 2, Pt. 5. 1912, *C. d.*, Wundsch, Zool. Anz., 39, p. 729, f. 1–16. 1913, *C. d.*, Wundsch, Z. Fisch., 14, p. 136, f. 1. 1914, *C. c.* and *C. c.* f. *d.*, Behning, Zool. Jb., 37, p. 385, f. A–N. 1914, *Cyrtophium spongicola*, Welitchkovsky, F. d. dist. Walonyki. Gouv. Woronege. Charkof, 12. 1915, *C. c.* and *C. c.* f. *d.*, Wundsch, S. B. Ges. Naturf. Fr. Berl., No. 3, pp. 56–81, Pl. 4, 5, Text-f. 1–9. 1919, *C. c.*, Wundsch, Arch. Hydrobiol. Plankt., 12, p. 693. 1923, *C. c.* f. *d.*, Kulmatycki, Arch, Rybact. Polsk., 4. 1923, *C. c.* f. *d.*, Schlienz, Arch. Hydrobiol., 14, p. 429. 1924, *C. c.*, Behning, Int. Rev. Hydrobiol., 12, p. 228. 1924 (a), *C. c.* prn. *f.*, Martynov, Russk. Gidrobiol. Zh., 3, p. 213. 1924 (b), *C. c.* subsp. *s.* and *C. c.* subsp. *s.* prn. *d.*, Martynov, Annu. Mus. Zool. Acad. Sci. Leningrad, 25, p. 49. 1925, *C. c.* f. *d.*, Kulmatycki, Arch. Rybact. Polsk. 1925, *C. c.*, Medwedewa, Arb. Biol. Wolga. Sta., 8, pp. 105–115. 1927, *C. c.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 84, p. 142. 1928, *C. c.*, Behning, Russk. Gidrobiol. Zh., 7, p. 263. 1928, *C. c.*, Behning, Binnengewasser, 5, Leben des Wolgas. 1929, *C. c.*, Stephensen, Die Tierwelt der Nord und Ostsee, 14, x, f., pp. 168–70, f. 40. 1930, *C. c.* f. *d.*, Kulmatycki, Frag. Faun. Mus. Zool. Polon., 1, No. 5. 1930, *C. c.*, Wolski, Frag. Faun. Mus. Zool. Polon., 1, p. 152. 1931, *C. c.* f. *d.*, Kulmatycki, Frag. Faun. Mus. Zool. Polon., 1, No. 11. 1931, *C. c.* f. *d.*, Kulmatycki, Verh. Int. Vereinig. Limnol. Stuttgart., 14, p. 429. 1935, *C. c.* f. *d.*, Crawford, Nature, 136, p. 685.

This variable, adaptable, and widely distributed species is found in salt, brackish, and fresh water, and several varieties have been described. Martynov (1924, *b*) restricts the use of the name *curvispinum* to specimens from the Caspian Sea, and employs a new name, subsp. *sowinskyi*, for specimens from the Black Sea. The name *devium* of Wundsch he applies to specimens from the R. Don, and rivers to the west of it, and considers these to form a "praenatio" of subsp. *sowinskyi*. He did not examine specimens from the Volga. The praenatio *fluviatilis* from the R. Oskol is described by Martynov (1924, *a*) from the figures of Welitchkovsky (1914), who named his specimens *Cyrtophium spongicola* n. sp.

This complicated scheme has not been adopted by any other writer. Wundsch regards *C. curvispinum* as an inhabitant of the Caspian Sea and Black Sea, and uses the name *C. curvispinum* forma *devium* for examples from fresh water; other authors follow this plan, or use the name *C. curvispinum* for all specimens.

Good accounts of the local races of this species are given by A. Behning (1914) (Caspian, Volga delta, Volga at Saratow, Black Sea, Dnieper at Kiev) and H. H. Wundsch (1919) (Caspian, Dnieper at Kiev, Muggelsee. near Berlin).

DISTRIBUTION. Caspian Sea (type locality) and the Volga to 2,772 km. from the mouth; Black Sea and lowland courses of Danube, Dnieper and Don; rivers emptying into the Baltic and North Sea (Niemen to Elbe): also two lakes in the Caucasus. England: River Avon at Tewkesbury; Crawford (1935).

Wolski (1930) gives the most up-to-date list of localities. Wundsch (1915) states that *C. c.* var. *devium* was at that time spreading rapidly in Germany, moving through canals and rivers from East to West, usually downstream. The English specimens (13 in number, both sexes) were identified by Prof. Wundsch as *C. curvispinum* var. *devium.*

ECOLOGY. Forming tubes on weeds in sluggish waters. *C. c.* var. *devium* is restricted to the freshwater lowland courses of rivers.

9. COROPHIUM MONODON G. O. Sars.

[Sars, G. O., 1895, p. 309, pl. 24, f. 8–16.]

1906, *C. m.*, Stebbing, Das Tierreich, 21 (1), p. 690. 1908, *C. m.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1924, *C. m.*, Spandl, S. B. Akad. Wiss. Wien., 133, pp. 476, 500.

DISTRIBUTION. Caspian Sea.

10. COROPHIUM MAEOTICUM Sowinski.

[Sowinski, W., 1898, Bull. Acad. Sci. St. Petersb., v. 8, p. 362, pl. 1, f. 1–5.]

1906, *C. m.*, Stebbing, Das Tierreich, 21 (1), p. 740. 1924 (*a*), *C. m.*, Martynov, Russk. Gidrobiol. Zh., 3, p. 210. 1924 (*b*), *C. m.*, Martynov, Annu. Mus. Zool. de L'Acad. Sci. Rus., 25, p. 44.

DISTRIBUTION. Sea of Azov. Penetrates some way into the R. Don, and builds tubes on *Cordylophora lacustris* and *Plumatella repens*, presumably in fresh water (Martynov, 1924, *b*).

11. COROPHIUM SALMONIS Stimpson.

[Bradley, J. C., 1908, p. 235, f. 20–35, 38, 39.]

1906, *C. s.*, Stebbing, Das Tierreich, 21 (1), p. 692.

DISTRIBUTION. California: Puget Sound. Alaska: Karluk beach and estuary (from stomachs of sockeyes and cohos—*Oncorhynchus nerka* and *O. kisutch*).

12. Corophium spinicorne Stimpson.

[Bradley, J. C., 1908, p. 287, f. 1–19, 36, 37.]

1888, *C. s.*, Stebbing, Rep. Voy. Challenger, 29, p. 303. 1906, *C. s.*, Stebbing, Das Tierreich, 21 (1), p. 692. 1925, *C. s.*, Essig, Pan. Pacif. Entom., 1, p. 189.

DISTRIBUTION. San Francisco Bay (salt-marshes): San Francisco water supply—one specimen, from fresh water, recorded by Essig and identified by C. R. Shoemaker of the Washington Museum.

13. Corophium affine Bruzelius.

[Sars, G. O., 1894, p. 618, pl. 221, f. 2.]

1862, *C. a.*, Bate, Cat. Brit. Mus., p. 283. 1901, *C. a.*, Elliott, Laurie and Murdoch, F. Fl. and Geol. Clyde Area, Glasgow, p. 343. 1905, *C. a.*, Scott, Proc. Roy. Phys. Soc. Edinb., 16, pp. 172–3. 1906, *C. a.*, Stebbing, Das Tierreich, 21 (1), p. 688. 1908, *C. a.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1927, *C. a.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 84, p. 139. 1929, *C. a.*, Stephensen, Die Tierwelt der Nord und Ostsee, 14, x. f., pp. 168–9, f. 40. 1929, *C. a.*, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Crustacea Amphipoda, pp. 1–40. 1933, *C. a.*, Stephensen, Fauna Arctica, 6, p. 372.

DISTRIBUTION. Europe: Lofoten Is. to N. Friesian Is.; Skagerrak, and N. Kattegat; Scotland (Firth of Forth, Firth of Clyde, Shetland Is.); Faroe Islands. A record by Sowinsky (1898) from the Bosphorus, in Mém. Soc. Kiev, v. 15, p. 457, is based on a single specimen which was not figured, and was lost. It probably did not belong to this species.

ECOLOGY. *C. affine* burrows in the sea-bottom in depths of from 8–60 m. (Stephensen, 1929).

14. Corophium aculeatum Chevreux.

[Chevreux, E., 1908, pp. 70–72, f. 1–3.]

1911, *C. a.*, Chevreux, Mem. Soc. Zool. Fr., 23, pp. 270–1.

DISTRIBUTION. Bône (Algeria) dredged from soft grey mud in about 8 m. of water.

IDENTIFICATION. The male is distinguished by the great length of its rostrum from all other males in this section.

15. Corophium annulatum Chevreux.

[Chevreux, E., 1908, pp. 73–74, f. 4, 5.]

1911, *C. a.*, Chevreux, Mem. Soc. Zool. Fr., 23, p. 271.

DISTRIBUTION. As for *C. aculeatum*.

I have seen specimens identified by M. Chevreux. The broadly truncate rostrum and the outgrowth near the base of the inner edge of antenna I, segment 1, distinguish the adult male of this species from all others in this section.

16. Corophium runcicorne Della Valle.

[Della Valle, A., 1893, p. 13, pl. 4, f. 7; pl. 8, f. 1–16, 19.]

1906, *C. r.*, Stebbing, Das Tierreich, 21 (1), p. 689. 1908, *C. r.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1908, *C. r.*, Chevreux, Bull. Soc. Zool. Fr., 33, p. 69. 1911, *C. r.*, Chevreux, Mem. Soc. Zool. Fr., 23, p. 270. 1925, *C. r.*, Chevreux, Bull. Soc. Zool. Fr., 50, p. 392. 1925, *C. r.*, Chevreux and Fage, F. de France, 9, p. 365, f. 373. 1925, *C. r.*, Schellenberg, Meeresf. W. Afrikas, 3, p. 191.

DISTRIBUTION. Mediterranean Coasts: Naples, Bonifacio, Algiers, Bosphorus.

ECOLOGY. Burrows in sand in 15–80 m.

IDENTIFICATION. The male is uniquely characterized by a curved, forwardly-pointing outgrowth from the base of the outer edge of antenna I, segment 1.

17. Corophium rotundirostre Stephensen.

1915, *C. r.*, Stephensen, Rep. Danish Oceanogr. Exped. Medit., 2, D. 1, p. 52, fig. 33.

DISTRIBUTION. Mediterranean, off the coast of Sicily (37°29′ N., 12°34′ E.).

ECOLOGY. Burrowing in clay in 112 m.

IDENTIFICATION. Only two specimens were found (1 male, 1 female) and these both lacked antenna II. In other features they rather resembled *C. annulatum*, but were far bigger (4–5·5 mm., compared with 1·5–2 mm. in length).

18. Corophium triaenonyx Stebbing.

[Stebbing, T. R. R., 1904, Spol. Zeyl., v. 2, p. 25, pl. 6 A.]

1906, *C. t.*, Stebbing, Das Tierreich, 21 (1), p. 740. 1908, *C. t.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 229. 1922, *C. t.*, Chilton, Trans. Proc. N.Z. Inst., 53, pp. 232–3.

DISTRIBUTION. Ceylon: L. Negombo.

ECOLOGY. Forming tubes under bark of coconut piles, in brackish water.

IDENTIFICATION. The male is not distinctive, but the female is characterized by the spines on antenna II, segment 4, which lie in a row of six or so along the lower edge, and a row of two on the inner surface.

19. Corophium rioplatense Giambagi.

[Giambagi, D., 1926, An. Mus. Nac. Buen. Aires, v. 34, p. 137, f. 1–3.]

1934, *C. r.*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 23.

DISTRIBUTION. Rio de la Plata.

ECOLOGY. Forming tubes on bivalve shells in fresh water.

IDENTIFICATION. The male is not distinctive, but the female is characterized by a laminar expansion running the length of antenna II, segment 4, and bearing four or five spines. This expansion is particularly pronounced distally.

Section B.

Urosome segments fused. Uropods I and II inserted in notches in the lateral margins of the urosome.

This section contains eight species, two of which (*C. sextoni* and *C. insidiosum*) are here described as new species. I have examined all except *C. californianum*. All are of small or moderate size, from 2 to 6 mm. in length. The male of *C. bonelli* and the female of *C. californianum* are unknown: in the other six species the 4th peduncular segment of antenna II is unlike in the two sexes. *C. crassicorne* burrows in muddy sand, the remainder build tubes on hydroids, etc. *C. bonelli*, *C. acherusicum*, and *C. insidiosum* are widely distributed. The section is confined to water of nearly full salinity, except for *C. insidiosum* which has frequently been found in salinities of about $15^\circ/_{\circ\circ}$.

KEY TO SPECIES.

1. Antenna II, segment 4 with a complex terminal tooth reaching nearly to end of segment 5 . . . *C. californianum* ♂
   Antenna II, terminal tooth on segment 4 absent, or not reaching middle of joint 5 . . . 2
2. Eye-lobes acute, eyes poorly developed; animal burrowing in muddy sand . . . 3
   Eye-lobes rounded or truncate, eyes well developed; animal building tubes upon sessile objects . . . 4
3. Antenna II, segment 4 with a large and a small terminal tooth . . . *C. crassicorne* ♂
   Antenna II, segment 4 armed with a row of 6–8 large spines . . . *C. crassicorne* ♀
4. Antenna II, segment 4 with a large terminal tooth and a smaller one above (♂) 5
   Antenna II, segment 4 armed only with spines (♀) . . . 9
5. Rostrum lanceolate, about $\frac{1}{3}$ as long as basal segment of antenna I . . . 6
   Rostrum triangular, short . . . 7
6. Antenna I, segment 1 with blunt outgrowth on inner surface about opposite middle of rostrum . . . *C. insidiosum* ♂
   Antenna I, basal segment with no such outgrowth . . . *C. uenoi* ♂
7. Antenna II, segment 4 very setose . . . *C. tuberculatum* ♂
   Antenna II, segment 4 with few, short setæ . . . 8
8. Antenna I, flagellum 5-segmented, <2nd segment; antenna II, segment 4 with 2–3 spines, segment 5 without processes . . . *C. sextoni* ♂
   Antenna I, flagellum 7–10-segmented, >2nd segment; antenna II, segment 4 without spines, segment 5 with 2 processes . . . *C. acherusicum* ♂
9. Antenna II, segment 5 without spines . . . *C. tuberculatum* ♀
   Antenna II, segment 5 with 1 or 2 spines . . . 10
10. Antenna II, segment 4 with spines set in a single row . . . 11
    Antenna II, segment 4 with all spines, except the terminal, set in pairs . 12
11. Antenna II, segment 4 with 4–6 spines set on a flange . . . *C. sextoni* ♀
    Antenna II, segment 4 cylindrical, with 3 spines . . . *C. uenoi* ♀
12. Antenna II, segment 4 with 3 pairs of spines, and a single terminal spine . *C. acherusicum* ♀
    Antenna II, segment 4 with 2 pairs of spines, and a single terminal spine . 13
13. Antenna I, segment 1 with the basal spines on inner and lower edges sharply recurved . . . *C. bonelli* ♀
    Antenna I, with these spines straight . . . *C. insidiosum* ♀

This key can only be satisfactorily used for adult specimens.

20. Corophium crassicorne Bruzelius.

Figure 4, a–f.

[Sars, G. O., 1894, p. 615, pl. 220.]

1862, *C. spinicorne* (♀) and *C. c.* (♂), Bate, Cat. Amph. Brit. Mus., pp. 281–2, pl. 47, f. 5, 6. 1888, *C. c.*, Robertson, Trans. Nat. Hist. Soc. Glasg., 2, p. 66. 1898, *C. c.*, Sowinski, Bull. Acad. Sci. St. Petersb., Ser. 5, 8, pp. 361–2. 1901, *C. crassicornis*, Elliott, F. Fl. and Geol. Clyde Area, p. 342. 1905, *C. c.*, Scott, Proc. R. Phys. Soc. Edinb., 16, p. 172. 1906, *C. c.* (part), Stebbing, Das Tierreich, 21 (1), p. 690 ("found in Norfolk in almost fresh water," refers to *C. lacustre*). ? 1907, *C. c.*, Norman, Ann. Mag. Nat. Hist., Ser. 7, 20, p. 369. 1908, *C. c.*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1914, *C. c.*, Walker, Spp. of Amph. and Isop. taken by Runa July–Aug., 1913. 1923, *C. c.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 78, p. 73. 1925, *C. c.*, Chevreux and Fage, F. de France, 9, p. 367, f. 375. 1927, *C. c.*, Stephensen, Vidensk. Medd. Naturh. Foren. Kbh., 84, p. 139. 1929, *C. c.*, Stephensen, Die Tierwelt der Nord-und Ost-See, 14, x. f., pp. 168–9, f. 40. 1929, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Amphipoda Crustacea, pp. 1–40. 1931, *C. c.*, Elmhirst, Proc. Roy. Soc. Edinb., 51, No. 21, p. 171. 1931, *C. c.* (part) Plymouth Marine Fauna, 2nd Ed. 1931, *C. c.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, No. 2, p. 168. 1932, *C. c.*, Elmhirst, Glasg. Nat., X, No. 2, pp. 56–62. 1933, *C. c.*, Stephensen, Fauna Arctica, 6, p. 372. 1934, *C. c.*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 24.

Papers by Hoek (1879, 89) placed by Stebbing (1906) in the synonymy of this species refer rightly to *C. acherusicum.*

DISTRIBUTION. Europe: "from Jan Mayen (not Greenland and Iceland) along the European coasts to Bosporus" –Stephensen (1929). America: Bay of Fundy to Gardiner's Bay, Long Island; Chichagof Harbour, Athi, Alaska—Shoemaker (1934).

ECOLOGY. *C. crassicorne* burrows in muddy sand, and is usually obtained by dredging in shallow water. At Fairlie Sands, Millport, in the Clyde, it is found between tidemarks, and I have seen a collection of 1,017 specimens taken from an area of 0·25 sq. metres from this locality.

I have dredged *C. crassicorne* at Plymouth in small numbers from Cawsand Bay, from White Patch, from near the Melampus buoy, and in the mouth of the Yealm. These grounds are all in shallow water (about 5 fm.) and the first three lie in Plymouth Sound. All four grounds are chiefly composed of fine sand and silt. Soil from Cawsand Bay contains 78% of fine sand and 19% silt, according to a determination made by the method of Allen (1899—Journ. Mar. Biol. Assoc., N.S., V, pp. 378–380). For soil from Melampus these figures are 37% and 6%, the remainder being chiefly formed by large stones between which this muddy sand is packed. Flourishing beds of *Zostera marina* (a plant also associated with *C. crassicorne* in the Clyde—Robertson, 1888) once existed at Cawsand, White Patch, and the mouth of the Yealm; in 1934–5 these had become much reduced.

Most of the records in Plymouth Marine Fauna (1931) probably refer to *C. bonelli*, as the localities given are suitable for this species and not *C. crassicorne.* Further I have found in the Laboratory at Plymouth jars of *C. bonelli* labelled *C. crassicorne.* The records of Percival (1929) must refer to *C. acherusicum* (p. 617), which I found abundant on the Neille Point buoys.

BREEDING AND SEX-RATIO. Ovigerous females were present in the collections made in April and July, but not in those made in October (26 specimens), November (9), or December (4). Of 67 specimens whose sex was determined 19·5% were males. Of 200 specimens examined from collections sent me from Millport, and collected in August, 1931, 49% were males.

IDENTIFICATION. The small eyes and sharp eyelobes are features not found in other species of this section. In the female the form of antenna II, segment 4, is distinctive at all ages; it is almost crescent-shaped in section, with the concavity facing inwards and upwards.

GROWTH-CHANGES. Juvenile females have fewer spines on the antennae than adults. In juvenile males the rostrum is less pronounced, and the spines on antenna I, which are short and blunt in the adult, are long and sharp: antenna II, segment 4, is relatively stouter than in the adult, and bears a few small spines on the ventral surface basally, which later disappear; there are no outgrowths on antenna II, segment 5. These changes are illustrated in Fig. 4, A–F. The larger specimen was 2·9 mm. long from rostrum to telson, and antennæ I and II were 53% and 70% of this length. For the other specimen these figures were 2·6 mm., 39% and 45%.

21. COROPHIUM BONELLI G. O. Sars.

Figure 2, H–O.

HISTORICAL. In 1830 Milne-Edwards gave the name *C. bonelli* to an Amphipod from an unknown locality, but his description is not precise enough for assured identification, and none of his specimens survive. In 1894 G. O. Sars described and figured female specimens of a Corophium collected in south-west Norway, which he called by Milne-Edwards' name. Neither of these authors makes mention of a male.

Though females continued to be found in great numbers, the first male to be assigned to this species was one collected in Alaska with three females, and described, but not figured, by Shoemaker (1920). In 1924 Stephensen figured one of a number of males from the east coast of Denmark, making mention in his description of the small differences between these males and the specimen examined by Shoemaker.

C. pseudacherusicum was named by Schellenberg (1931) from a few females from Tierra del Fuego. He noted a few slight differences between his specimens and the figures of Sars.

EXAMINATION OF SPECIMENS. Thanks to the kindness of Dr. Huus of Oslo, Dr. Stephensen of Denmark, Prof. Schellenberg of Berlin, Dr. Panning of Hamburg, Prof. Fage of Paris, Prof. Brian of Genoa, Prof.

Dohrn of Naples, and Dr. Shoemaker of Washington, I have been able to examine specimens from many parts of the world, as noted in Appendix I (a) and (b).

I found that :—

(1) The females could be separated into two forms, never both present in the same collection. The small but constant differences between them are tabulated in Table II.

(2) Of these forms none was ever found with males in the same collection, even when present in thousands (except occasionally with males of *C. sextoni*, *C. acherusicum*, or *C. acutum*). A list of specimens of this form is given in Appendix I (a).

(3) To this form belonged all the females identified with *C. bonelli* by G. O. Sars. They are 164 in number, from four localities in south-west Norway, and are now at the Oslo Museum.

Sars did not set apart a type, and therefore I have considered all these specimens as co-types of the species. They resemble his figures and description so closely that I have no doubt, in view of the evidence of locality, that figures, description and specimens belong all to a single species, which I shall call *C. bonelli* G. O. Sars, to avoid confusion with Stephensen's use of the name *C. bonelli* (M.-Edw. ?) G. O. Sars. There are, however, some slight differences, in features important for diagnosis, between Sars' figures and his specimens, and I have therefore redescribed *C. bonelli* on page 613.

(4) To this form also belong the 15 specimens from Tierra del Fuego, on which was based Schellenberg's description of *C. pseudacherusicum*. Schellenberg used Sars' figures and description for comparison with his specimens. From these he drew up the list of differences between his species and *C. bonelli*, with the exception of the difference in shape of the basal joint of the mandibular palp, for the observation of which he compared his specimens with some from the Kieler Bucht, Germany. These I have seen, and found to belong to the other form, which I have described on page 615 as *C. insidiosum* n.sp.

The specimens from Tierra del Fuego are indistinguishable from those of Sars. I therefore regard *C. pseudacherusicum* as a synonym of *C. bonelli* G. O. Sars.

(5) The other form of female was almost always found with males, which usually made up 20 40% of the whole number in a collection (see Appendix I (b)). Adult males were not distinguishable from that figured by Stephensen (1924) as *C. bonelli* (M.-Edw. ?) G. O. Sars, and all certainly belonged to one species, as the whole range of variation was sometimes represented in single large collections.

TABLE II.

	C. bonelli G. O. Sars (ovigerous ♀♀). Norway (G. O. Sars det.), England, France, Denmark, East Coast of N. America.	*C. insidiosum* n. sp. (ovigerous ♀♀). Plymouth, Venice, Denmark, Germany.
Antenna I, joint 1, spines on lower edge	4, rarely 5, never 3; distal 3 straight, basal 1 or 2 sharply recurved.	3 or 4, rarely 5; all straight.
Antenna I, joint 1, spines on inner edge	1–3; basal 1 sharply recurved.	1–3; basal 1 not, or slightly, recurved.
Antenna II, joint 5, spines on lower edge	2, less frequently 1.	1; in 2 out of 400 specimens, 2.
Mandibular palp, basal joint	Distinctly prolonged.	Not distinctly prolonged.
*Gnathopod I, palm	Very oblique; spines stout, those near the hinder edge far the longest.	Nearly straight: spines slender, of uniform size.
Gnathopod II, accessory teeth on dactyl	2, rarely 1.	3, rarely 2 or 4.
*Uropod I, spines on inner edge of peduncle	3 or 4, well spaced.	1, terminal.

* These distinctions are based on an investigation of *C. bonelli* from Norway and Plymouth and *C. insidiosum* from Plymouth and the Lake of Venice only.

The specimens described by Shoemaker (1920) do not fit into this scheme. I have not seen them, but Dr. Shoemaker has sent me excellent tracings of the most important features. Both sexes differ from *C. insidiosum* in having the basal joint of the mandibular palp much prolonged, and the dactyl of gnathopod II with only one accessory tooth. The other features of the male considered by Shoemaker (1934a) to be

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EXPLANATION OF FIGURE 2.

A–E.—*Corophium insidiosum* n.sp.,♀ holotype × 52.
- A.—Antenna I, segment 1 from side.
- B.—Antenna I, segment 1 from above.
- C.—Antenna II.
- D.—Gnathopod I, propod.
- E.—Gnathopod II, dactyl.

F.—♀ paratype, Plymouth, mandibular palp × 250.

G.—♂, L. of Venice, mandibular palp × 250.

H–O.—*C. bonelli* G. O. Sars.

H–J.—Ovigerous ♀, Millbay, Plymouth, 22.vii.07.
- H.—Mandibular palp × 250.
- I.—Antenna II × 38.
- J.—Antenna I, segment 1 and 2, from above, × 38.

K–M.—Ovigerous ♀, Tierra del Fuego, 30.x.1892, Hamburg Museum 10752 (co-type of *C. pseudacherusicum*), × 38.
- K.—Antenna II.
- L.—Antenna I, peduncle, from side.
- M.—Antenna I, from above.

N, O.—Ovigerous ♀, Norway (determined by Sars as *C. bonelli*), × 38.
- N.—Antenna I, from side.
- O.—Antenna II.

P.—*C. acherusicum* da Costa, ♀, Neille Pt., Plymouth, 29.1.35, antenna II (setae omitted) with an exceptionally large number of spines, × 38.

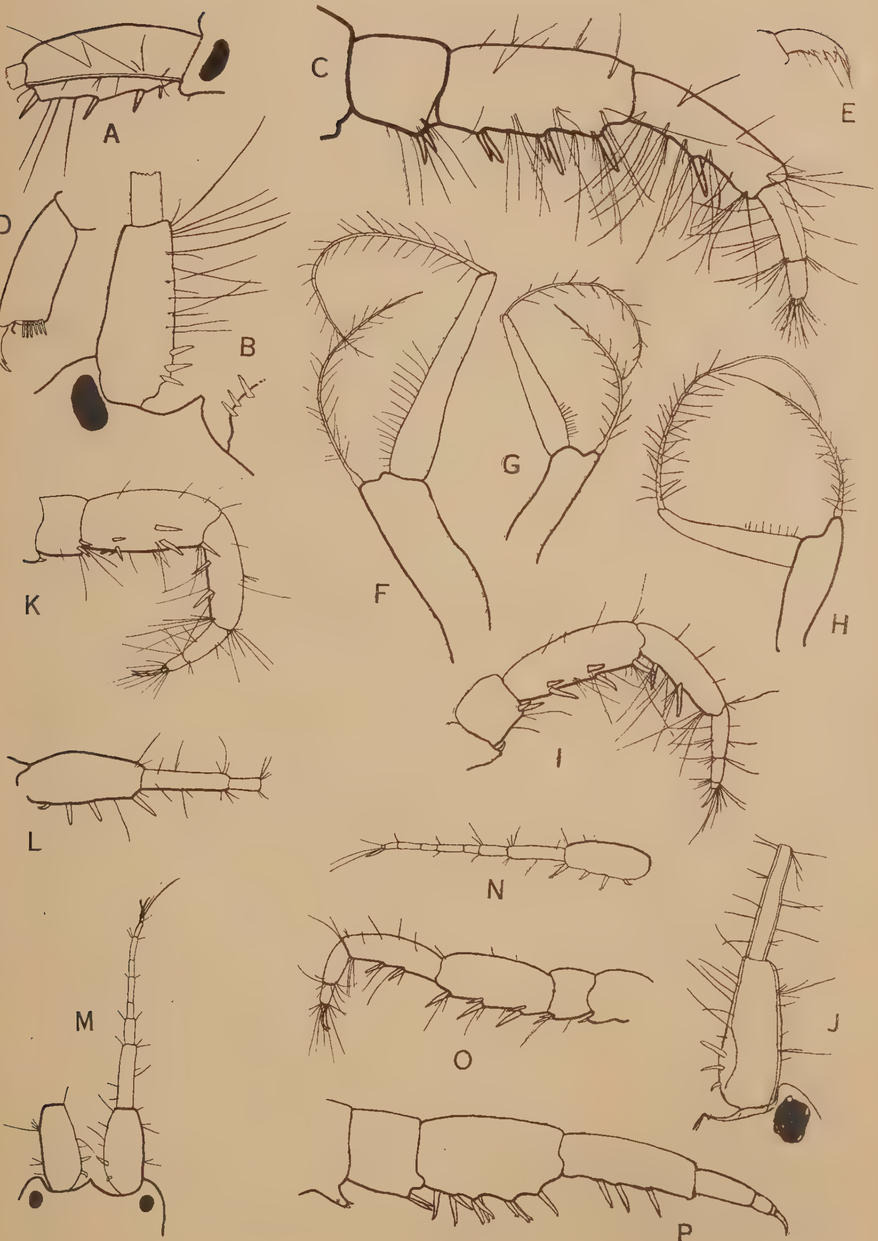
A
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Fig. 2.

distinctive are also found in juvenile males of *C. insidiosum*, and the antennae of the female resemble those of *C. insidiosum* in the number and arrangement of spines. Until more material is obtained the precise status of these specimens must be uncertain. They certainly closely resemble *C. insidiosum* in both sexes, but appear to be distinct.

REFERENCES. Owing to the confusion between *C. bonelli* and *C. insidiosum* it is frequently impossible to tell to which of these species a paper refers.

References presumably applicable to C. bonelli only.

? 1830, *C. b.*, Milne Edwards, Ann. Sci. Nat., 20, p. 385. ? 1840, *C. b.*, Milne Edwards, Hist. Nat. Crust., 3, p. 67. ? 1862, *C. b.*, Bate, Cat. Amph. Brit. Mus., p. 282. ? 1873, *C. b.*, Parfitt, Trans. Dev. Ass. Sci. and Lit., 6, p. 249. 1879, *C. crassicorne* var., Hoek, Tijdschr. Ned. Dierk. Ver. IV, p. 118, Pl. 8, f. 9, 10. 1882, *C. b.*, Sars, Vid. Selsk. Forh. Christ., No. 18, p. 112. 1889, *C. c.*, Walker, 3rd Rep. Higher Crust., L. M. B. C. distr. Liverpool, p. 211. ? 1893, *C. b.*, Chevreux and Bouvier, Ann. Sci. Nat., Ser. 7, 15, p. 140. 1893, *C. b.*, Della Valle, F. Fl. Neapel, 20, p. 368. 1894, *C. b.*, Sars, Crust. Norway, 1, p. 616, pl. 221, f. 1. ? 1897, *C. b.*, Sowinski, Mém. Soc. Kiew, 15, p. 456. ? 1900, *C. b.*, Chevreux, E., Rés. Comp. Sci. Monaco, 16, p. 109. ? 1901, *C. b.*, Elliott, Laurie and Murdoch, F. Fl. Geol. Clyde Area, Glasgow, p. 343. 1905, *C. b.*, Scott, Proc. R. Phys. Soc. Edinb., 16, p. 172. 1906, *C. b.*, Norman and Scott, Crust. Devon and Cornwall, p. 95. 1906, *C. b.*, Stebbing, Das Tierreich, 21 (1), p. 691. ? 1907, *C. b.*, Norman, Ann. Mag. Nat. Hist., Ser. 7, 20, p. 369. 1910, *C. b.*, Chevreux, Mém. Soc. Zool. Fr., 23, p. 271. 1914, *C. b.*, Walker, Ann. Mag. Nat. Hist., Ser. 8, 13, p. 558. 1929, *C. b.*, Stephensen, Zoology of Faroes, Copenhagen, XXIII, Marine Crustacea Amphipoda, pp. 1–40. 1930, *C. b.*, Barnard, Brit. Ant. Terra Nova Exp., Nat. Hist. Crust., XI, p. 393. 1931, *C. b.*, and *C. crassicorne* (part), Plymouth Marine Fauna, p. 197. 1931, *C. pseudacherusicum*, Schellenberg, Furth. Zool. Res. Swed. Antarct. Exp. 1901 3, No. 6, p. 258, f. 1932, *C. cylindricum*, Barnard, Disc. Rep. V, p. 244. 1933, *C. b.*, Stephensen, Fauna Arctica, 6, p. 372.

References to C. bonelli and C. insidiosum, with confusion between the species.

1924, *C. b.*, Stephensen, Vidensk. Medd. Naturh. Forening, Copenhagen, 78, pp. 73–78, f. 3. 1924, *C. b.*, Ussing, Tom. cit., pp. 69–72. 1925, *C. b.*, Chevreux and Fage, F. France, 9, Amph., p. 369, f. 377. 1927, Stephensen, Tierwelt Nord und Ostsee, 14, x. f., pp. 168–9. 1931, *C. b.* and *C. pseudacherusicum*, Schellenberg, Furth. Zool. Res. Swed. Antarct. Exp., 6, p. 258. 1931, *C. b.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, pp. 168–70. 1932, *C. b.*, Brian, Boll. Mus. Zool. Anat. Comp. Genova, 12, No. 52. 1934, *C. pseudacherusicum*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 26.

Table III shows my interpretation of the meaning given to the names *C. bonelli* and *C. pseudacherusicum* in certain recent papers.

TABLE III.

Paper.	*C. bonelli* refers to :—	*C. pseudacherusicum* refers to :—
Shoemaker (1920) .	Sars' (1894) figures of *C. b.*, ♀; 1♂, 3♀♀ from Alaska (sp. indet.).	—
Stephensen (1924) .	Sars' figures of *C. b.*, ♀; ♂♂ and ♀♀ of *C. i.* from Denmark.	—
Schellenberg (1931).	Sars' figures of *C. b.*, ♀; ♀♀ of *C. i.* from Germany.	*C. b.* from Tierra del Fuego.
Brian (1932) . .	♂♂ and ♀♀ of *C. i.* from L. of Venice; Sars' observations on sex-ratio of *C. b.*	—
Shoemaker (1934). .	As Shoemaker (1920)	♂♂ of *C. i.* from Denmark; ♀♀ of *C. b.* from Tierra del Fuego and N. America.

Brian's statement that *C. bonelli* is an example of "geographic parthenogenesis" is due to a confusion of this species with *C. insidiosum*. So is the observation by Shoemaker (1934a) that the form of the mandibular palp is different in the two sexes of *C. pseudacherusicum*.

REDESCRIPTION OF FEMALE OF *C. bonelli* G. O. SARS (Fig. 2, H–O), from specimens from Norway named by G. O. Sars.

Length about 4 mm. in ovigerous females. *Rostrum* short, triangular. *Eyes* black, well-developed. *Eyelobes* rounded.

Antenna I: segment 1 $<2+3$, lower edge with three large, straight, equally spaced spines distally and one or two shorter, sharply recurved spines proximally; inner edge with one to three spines, proximal one short and sharply recurved; flagellum, 8-segmented in fully grown specimens.

Antenna II: segment 4 with a basal and a median pair of spines and a terminal single spine, on the lower edge; segment 5 frequently with two spines of which the proximal is sometimes as large as the distal, sometimes smaller or absent even in the largest specimens—the distal spine is always present.

Mandibular palp, basal segment much prolonged beyond base of second segment. *Gnathopod I*, palm very oblique, with a row of stout spines of which those near the hinder edge of propod are far the largest; dactyl with one small accessory tooth. *Gnathopod II*, dactyl with two, or more rarely one, accessory tooth.

Urosome segments fused; sides of urosome hollowed out at the insertion of uropods 1 and 2.

The male is unknown. Since the female has been collected, often in thousands, from many parts of the world, it is very probable that reproduction in this species is normally parthenogenetic. This has never, however, been tested by rearing experiments. Parthenogenesis is known in *Talitrus alluaudi* Chevreux, and there is some evidence for it in *Haustorius arenarius* (Slabber), but it is certainly unusual in the Amphipoda. There is no reason to suppose that it occurs in any other known species of Corophium.

DISTRIBUTION. See Appendix I (a).

OCCURRENCE AT PLYMOUTH. In the Laboratory at Plymouth are several collections made between 1889 and 1911, chiefly from Millbay Channel, but also from Asia Shoal, West Channel, and between Drake's Island and Mount Edgecumbe. Each of these contains several hundreds of specimens.

In 1934 from several dredgings on these grounds I obtained only five specimens, four from New Grounds and one from near Drake's Island. The place of *C. bonelli* was taken by *C. sextoni* n.sp., a species not present in the earlier dredgings.

C. bonelli builds tubes of mud on hydroids, etc., in water usually of full salinity. Breeding females are present in collections made at Plymouth in April, July, August, and October.

IDENTIFICATION. This species has often been confused with *C. crassicorne* and *C. acherusicum*. *C. crassicorne* is easily distinguished by its burrowing habits, the pointed eyelobe and by antenna II, segment 4, which in the female is expanded along its lower edge into a broad flange on which about eight spines are set in a row. Many of the distinctions between *C. acherusicum* and *C. bonelli* tabulated by Chevreux (1911) and Stephensen (1924) do not hold good for specimens of *C. bonelli* as redescribed here. The species are, however, distinct, and ovigerous females may be identified from Table IV. Younger specimens of either species have fewer spines.

TABLE IV.

	C. bonelli ♀.	*C. acherusicum* ♀.
Antenna I	>antenna II, peduncle.	<antenna II, peduncle.
Antenna I, segment 1	<2+3.	>2+3.
Antenna I, segment 1, inner and lower edges	Basal spines sharply recurved.	All spines straight.
Antenna II, segment 4	5 spines, arranged 2, 2, 1.	7 spines, arranged 2, 2, 2, 1.
Pereiopod 7	Basal joint<propod.	Basal joint>propod.

VARIATION AND GROWTH CHANGES. As indicated in the redescription of this species on page 613 the number of spines on the antennal segments is not constant even in adults: in juveniles several spines are usually absent, especially the proximal spines of antenna I, and antenna II, segment 4. In very small specimens (*ca.* 1·5 mm.) the proximal spine of antenna II, segment 5, is missing, and it frequently does not develop at all. Adult specimens are common in which the proximal spine is smaller than the distal, or in which it is absent from one antenna and present on its fellow. The percentage of ovigerous females in which it was found varied in collections from different localities, but not in correlation with latitude. The highest figure was 77 (from Plymouth), and the lowest 20 (from Trondhjem Fjord, Norway); however, figures greater than 70 were obtained from some Norwegian collections. Occasional specimens bear an additional spine beside the median pair on antenna II, segment 5, but the number is far less variable than in *C. acherusicum*. The number of accessory teeth on the dactyl of gnathopod II is usually two in ovigerous females and one in small specimens.

22. Corophium insidiosum n.sp.

Figure 2, A–G.

DESCRIPTION OF FEMALE HOLOTYPE (Fig. 2, A–E). West Wharf, Millbay, Plymouth, 8.v.35, ovigerous.

Length 4·5 mm. *Rostrum* pointed, short. *Eyelobes* rounded, elongate. *Eyes* black, well developed.

Antenna I: about 30% of total length; segment 1 $<2+3$; lower edge with four straight spines, proximal one small, and a few long setae; inner edge with three straight spines near base, several long setae distally; outer edge with scattered short setae; segment 2 cylindrical, with several tufts of long setae; flagellum 7-segmented.

Antenna II: scarcely longer than antenna I; segment 4 with 5 spines on lower edge—a basal and a median pair and a single terminal spine—besides many long setae; segment 5 with one median spine, and many long setae; flagellum 3-segmented.

Mouth-parts and limbs in general like those of *C. bonelli*. *Mandible*, palp with basal segment not prolonged. *Gnathopod I*, palm almost square, with six slender spines of uniform size on each face; dactyl with a minute accessory tooth. *Gnathopod II*, right dactyl (figured) with four accessory teeth; left dactyl with the more usual number, three. *Pereiopod* 7, basal segment oval=propod in length.

Urosome as in *C. bonelli*. *Uropod I*, peduncle with one terminal spine on inner edge. *Telson* trapezoidal, with a wide terminal furrow, bordered with hooked spines.

DESCRIPTION OF MALE PARATYPE. West Wharf, Millbay, Plymouth, 8.v.35.

Length 3·5 mm. *Rostrum* spear-shaped, reaching nearly half-way along antenna I, segment 1; depressed at tip.

Antenna I: about 50% total length; segment 1, lower edge with a keel bearing one small terminal spine, and a few long setae; inner edge with only a few short setae—between these edges on the inner face a symmetrical blunt process opposite a point between the middle and tip of rostrum; outer edge with scattered short setae: segment 2=segment 1, narrowed at base, with a keel below bearing 16 long setae, rounded above with scattered setae of medium length: segment 3 $<\frac{1}{2}$ segment 2; flagellum 10-segmented, $<$segments $1+2$.

Antenna II: about 60% total length; segment 4, very stout, with a single large terminal ventral tooth, above which is a smaller single tooth; with only a few setae: segment 5, cylindrical, lower edge with a uniform series of eight tufts of long setae: flagellum, 3-segmented, basal segment with a row of five tufts of long setae.

Other features as in female.

I have not figured the male, since all characters of importance are excellently drawn by Stephensen (1924).

DISTRIBUTION. See Appendix I (b).

ECOLOGY. *C. insidiosum* like *C. bonelli* builds tubes of mud on weeds or hydroids ; it appears, however, to frequent as a rule water that is less saline. The most nearly marine conditions under which I have found it at Plymouth are at Tinside, and at Millbay Pontoon and West Wharf. These are subject to a considerable diminution in salinity when the Tamar is running full. Millbay Inner Basin is an enclosed brackish pool. The buoys at Bull Point and Neille Point lie some miles up the Tamar Estuary. Chelson Meadow is reclaimed land : the ditches are brackish, filled by land drainage and occasionally by salt water coming over the sea-wall. Here *Corophium insidiosum* was found in numbers, building tubes on *Ruppia maritima* in the most saline ditches, that is to say those nearest the sluice which opens into the Plym Estuary. In the same collections *Sphaeroma hookeri* (Isopoda) was abundant, and a few *Melita palmata* and *Leptocheirus pilosus* (Amphipoda) were present. A hundred yards from the sluice the numbers of Corophium were much reduced, and it was associated with large numbers of *Sphaeroma hookeri* and *Gammarus chevreuxi*.

Ussing (1924) observes that the optimum salinity for *C. bonelli* in the Mariagerfjord is 13–18$^\circ/_{\circ\circ}$. I have seen his specimens, and found them to be *C. insidiosum*. The Italian and German localities also appear to be estuarine rather than marine.

IDENTIFICATION. The very long rostrum of the male is not found elsewhere in this section except in *C. uenoi*, and in Shoemaker's undetermined specimens from Alaska. The outgrowth on the inner surface of antenna I, segment 1, is absolutely distinctive.

The arrangement of spines on the antennae of ovigerous females is sufficient for identification.

23. COROPHIUM UENOI Stephensen.

1932, *C. u.*, Stephensen, Annot. Zool. Jap., 13, p. 494–8, f. 3, 4.

DISTRIBUTION. Japan, in a tidal pool, presumably a tube-builder.

IDENTIFICATION. This species is very close to *C. bonelli* and *C. insidiosum*, from both of which it is distinguished by the female having only three spines, set in a longitudinal row, on antenna II, segment 4. In the type specimen brood-lamellae were developed, and presumably this arrangement of spines is typical of adult females. I have seen the male and cannot distinguish it from juvenile males of *C. insidiosum* ; from adult males it is distinguished by the absence of an outgrowth on the inner surface of antenna I, segment 1.

24. Corophium acherusicum Costa.

Figure 2, p.

[Della Valle, A., 1893, p. 364, pl. 1, f. 11 and pl. 8, f. 17, 18, 20–41.]

1862, *C. a.*, Bate, Cat. Brit. Mus., p. 282. 1873, *C. cylindricum*, Smith and Verrill, Rep. U.S. Comm. Fish., 1, p. 370. 1879, *C. crassicorne*, Hoek, Tijdschr. Ned. Dierk. Ver., 4, p. 115, pl. 5, f. 16; pl. 8, f. 4–8. 1880, *C. bonelli* (♀), *C. crassicorne* (♂), Sowinsky, Les Amph. du Golfe Sebastopol. Kiev., pp. 18–20, pl. 3, f. 3, 4. 1889, *C. crassicorne*, Hoek, Tijdschr. Ned. Dierk. Ver., Ser. 2, 2, p. 230. 1893, *C. cyl.*, Della Valle, F. Fl. Neapel, 20, p. 376. 1900, *C. a.*, Chevreux, Result. Camp. Sci. Monaco, 16, p. 109. ? 1904, *C. cyl.*, Holmes, Bull. U.S. Bur. Fish., 24, p. 521, figs. 1905, *C. cyl.* (part), Paulmier, F. C., Bull. N.Y. St. Mus., 91, Zool., 12, p. 167 (see notes on literature below). 1906, *C. a.*, Stebbing, Das Tierreich, 21 (1), p. 692. 1908, *C. acheruzicum*, Bradley, Univ. Cal. Publ. Zool., 4, p. 230. 1908, *C. a.*, Chevreux, Bull. Soc. Zool. Fr., 33, p. 69. 1911, *C. a.*, Chevreux, Mém Soc. Zool. Fr., 23, p. 271. ? 1914, *C. cylindricus*, Stebbing, Proc. Zool. Soc. Lond., p. 341. 1914, *C. a.*, Walker, Ann. Mag. Nat. Hist., Ser. 8, 13, p. 558. 1916, *C. a.* (part), Barnard, Ann. S. Afr. Mus., 15, p. 272 (see notes on literature below; see also *C. acutum*). 1918, *C. cyl.*, Kunkel, Bull. Conn. Geol. Nat. Hist. Surv., p. 171, f. 52. 1923, *C. a.*, Stephensen, Vidensk. Medd. Naturh. Foren., 78, p. 73. 1925, *C. a.*, Chevreux, Bull. Soc. Zool. Fr., 50, p. 392. 1925, *C. a.*, Chevreux and Fage, F. de France, 9, p. 368, f. 376. 1925, *C. a.*, Schellenberg, Meeresf. W. Afrikas, 3, p. 191. 1928, *C. a.*, Cecchini, Acc. Fisio. Crit. Siena (10), 3, p. 309. 1929, *C. crassicorne*, Percival, J. Mar. Biol. Assoc., 16, p. 81. 1931, *C. crassicorne* (part), Plymouth Marine Fauna, p. 197. 1931, *C. a.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, pp. 168–170. 1932, *C. bonelli*, Barnard, Disc. Rep., V, p. 244. 1934, *C. a.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 24–5. 1935, *C. a.*, Cecchini and Parenzan, Pub. Staz. Zool. Nap., 14, p. 227.

NOTES ON LITERATURE. Barnard (1916) records *C. acherusicum* from S. Africa. He describes antenna II, segment 5, in the male as bearing "in small specimens up to 2·5 mm., a well-marked tooth on lower margin about $\frac{1}{3}$ from base or sometimes nearly in the middle, in other and larger specimens without a tooth and much more sparsely setose." The smaller specimens are *C. acutum*, the larger *C. acherusicum*, and both these species are represented in collections from Durban sent by Barnard to the British Museum.

The figure given by Paulmier (1905) must be referred to *C. tuberculatum* Shoemaker, though the urosome segments have been drawn separate in error. Through the kindness of Dr. Stoner of the New York Museum I have been able to examine some of Paulmier's specimens; both *C. acherusicum* and *C. tuberculatum* were present in tubes labelled *C. cylindricum* by Paulmier.

DISTRIBUTION. Europe: S. England (Plymouth, Thames Estuary*); Coasts of France and Holland; Mediterranean. Africa: N. Coast from Suez Canal to Senegal, Durban Bay,* Dar-es-Salaam. America: Baffin's Bay to Brazil, ? Falkland Is., Cuba,* Alaska.* Asia: Hong Kong.* New Zealand: Lyttelton Harbour.*

ECOLOGY. *C. acherusicum* forms tubes on weed and hydroids in shallow water, usually in harbours, and especially on floating objects such as buoys.

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* Specimens examined in British Museum.

rafts, and pontoons. The Sheerness specimens are from fouling on a ship's bottom.

OCCURRENCE AT PLYMOUTH. Buoys and rafts: Tinside bathing raft; buoys at Neille Point, Saltash, Barn Pool; Millbay Pontoon. Intertidally in small numbers at Neille Point Mussel Bed. It was most abundant on the Neille Point buoy where thousands were obtained from a breffit of weed, and least common on Millbay Pontoon where it was outnumbered by *C. acutum*, *C. sextoni*, and *C. insidiosum*.

IDENTIFICATION. Normal ovigerous females bear seven spines on antenna II, segment 4, arranged 2, 2, 2, 1. Occasional specimens bear up to four additional spines on this segment either alongside an original pair of spines, or between two pairs. I have seen such specimens from Plymouth, Sheerness, the Lake of Venice, and Alaska. In some, antenna II, segment 5, bore three spines in a row. (See Fig. 2, P.)

Adult males may be known by the following combination of characters: rostrum short; antennae scarcely setose; antenna II, segment 5 with a small process near the base and a large blunt process terminally.

GROWTH-CHANGES. In the female the number of antennal spines, and of accessory teeth on the dactyl of gnathopod II, increase with age.

In the male there is a progressive deterioration of spines in number and size, and an appearance of processes on antenna II, segment 5, as shown in Table V.

TABLE V. (*C. acherusicum*, male).

	Juvenile 2–2·5 mm.	Adult 3–4 mm.
Antenna I, segment 1, spines on lower edge	3–4	1–4
Antenna II, segment 4, spines near base	1–2	0
Antenna II, segment 5, spines	0–2	0
Antenna II, segment 5, processes	0	small basal and large terminal.
Gnathopod II, dactyl, accessory teeth	1–2	2–3
Pereiopod 7, carpus inner edge	nearly straight	strongly convex

BREEDING AND SEX-RATIO. Most of the females found in August (1935) and September (1934) were ovigerous; in January (1935) adult

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EXPLANATION OF FIGURE 3.

Corophium sextoni n.sp.

A–F.—♀ holotype.
  A.—Antenna II, × 50.
  B.—Antenna I, segment 1 from inner side, × 50 (setae not drawn on inner or outer edge).
  C.—Head from above, × 50.
  D.—Mandibular palp, × 100.
  E.—Gnathopod II, dactyl, × 50.
  F.—Urosome, × 50.
G. H.—♂ paratype, × 50.
  G.—Antenna II.
  H.—Uropods I and II.

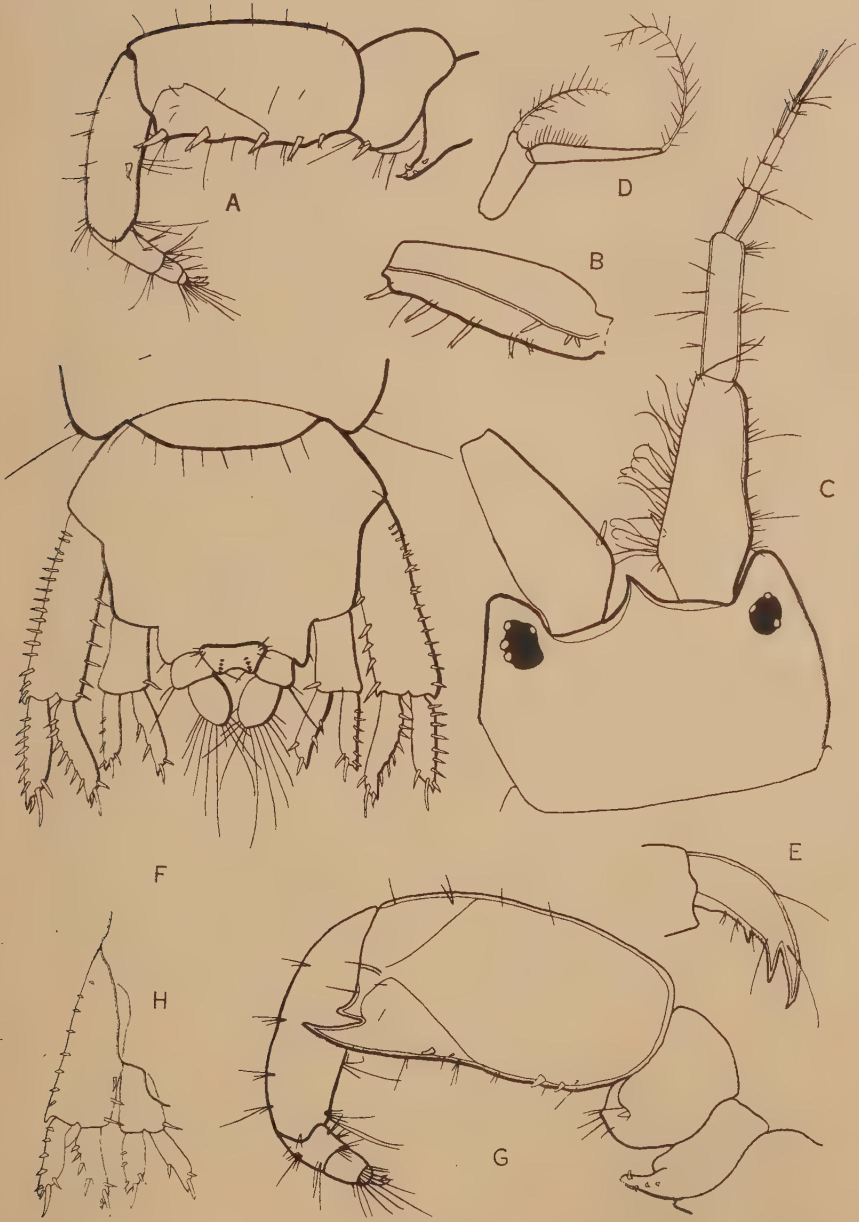

FIG. 3.

females were much outnumbered by juveniles. Both sexes were present in all collections I examined, the female being rather the commoner.

25. Corophium sextoni n.sp.

Figures 3, A–H; 4, G–H.

DESCRIPTION OF FEMALE HOLOTYPE (Fig. 3, A–F). Winter Shoal, Plymouth Sound, 18.x.34, ovigerous.

Length 4·5 mm. *Rostrum* short, triangular, acute. *Eye* large black. *Eyelobes* long, rounded.

Antenna I : about 30% of total length ; segment 1 $>2+3$; lower edge convex, with five spines of which the proximal one is very short and recurved, the distal ones progressively longer and straighter, two setae ; inner edge with two short recurved spines near base, beyond these a straight longer spine and 20–30 rather long setae ; outer edge with several short setae, and tufts of longer ones at $\frac{2}{5}$ and $\frac{3}{4}$; segment 2 with scattered setae ; flagellum 5-segmented, shorter than segment 2.

Antenna II : about 35% of total length ; segment 4 about twice as long as broad, pear-shaped in cross section with the lower edge produced into a flange running lengthwise and bearing five straight spines, increasing in length distally ; segment 5 rather stout, with a short straight median spine on the lower edge ; flagellum 3-segmented ; antenna as a whole with few setae, and those short.

Mouth-parts, *gnathopods*, and *pereiopods* resembling in general those of *C. bonelli*. *Mandibular palp*, segment 1 slightly produced terminally. *Gnathopod I*, dactyl with small accessory tooth ; propod with palm convex, oblique, set with several spines of which the posterior are largest, *Gnathopod II*, dactyl, with two subsidiary teeth. *Pereiopods* 5 *and* 6. spines on carpus short, in two rows.

Urosome segments fused, lateral border emarginate at insertion of uropods I and II. *Uropod I*, peduncle with five to six spines on inner

EXPLANATION OF FIGURE 4.

A–F.—*Corophium crassicorne* Bruzelius from Fairlee Sands, Millport, × 50.
A–C.—Adult ♂.
  A.—Antenna II.
  B.—Antenna I from above.
  C.—Antenna I from side (peduncle only).
D–F.—Juvenile ♂.
  D.—Antenna II.
  E.—Antenna I from above.
  F.—Antenna I from side (peduncle only).
G, H.—*Corophium sextoni* n.sp., ♂ paratype, × 50.
  G.—Head from side.
  H.—Head from above.

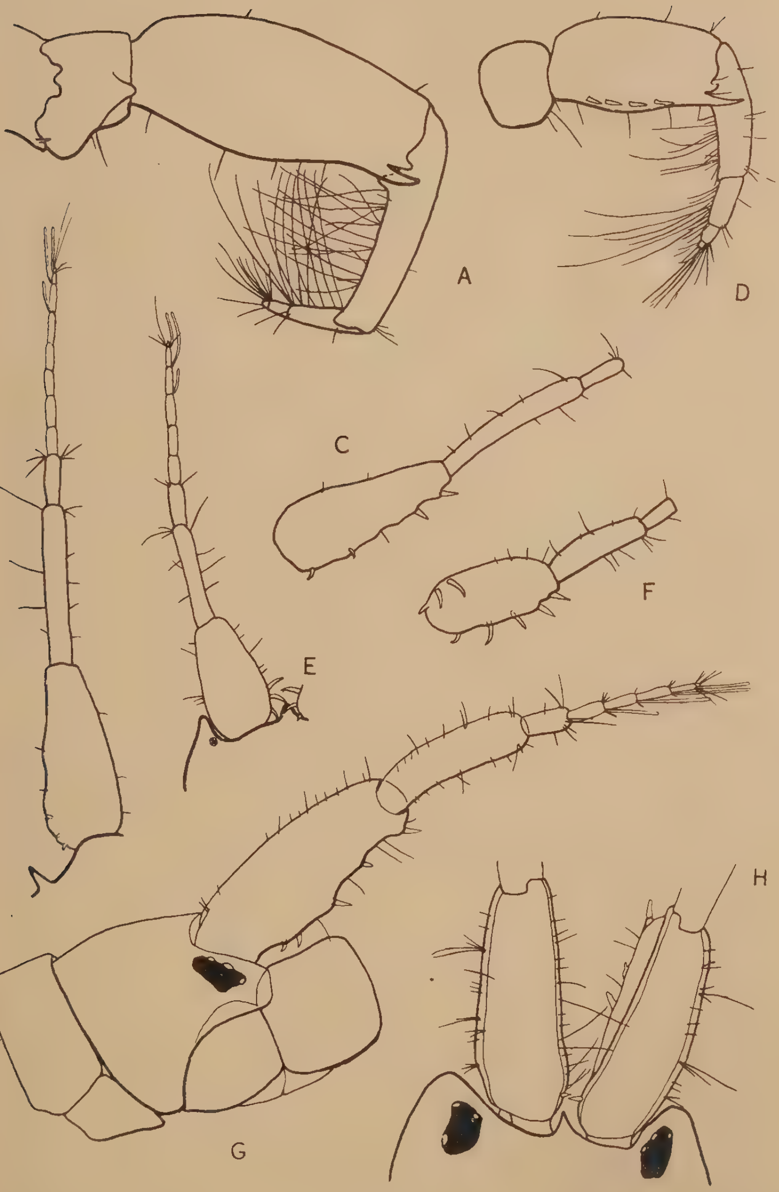

Fig. 4.

edge. *Telson* trapezoidal, with the terminal emargination bordered by four denticles on either side.

DESCRIPTION OF MALE PARATYPE (Figs. 3, G–H ; 4, G–H).

Length 4·0 mm.

Antenna I : about 40% total length ; segment 1 >2+3 ; lower edge convex with five small spines, of which the basal two are recurved, and a few setae ; inner edge with one small spine near base, and several setae beyond, mostly short ; outer edge with a few short setae ; segment 2 with a few short setae ; flagellum 5-segmented=segment 2.

Antenna II : about 55% length of animal ; segment 4 less than twice as long as broad, bearing at lower distal end a large tooth with a smaller tooth above it ; on the lower edge two short, stout spines or processes ; flagellum 3-segmented ; antennae as a whole with few setae, and those short.

Urosome as in female, but appendages less spinose.

Colour of paratypes in life : whitish grey, with two slaty bars across each segment, and slaty marking on antennae and head ; sexes similar. Eggs, bright pale yellow.

DISTRIBUTION. Plymouth ; Wembury (J. A. Kitching) ; off mouth of Tagus.*

ECOLOGY. Building tubes of mud on hydroids, sponges, weed from just above low-water mark to 25 fm.

OCCURRENCE AT PLYMOUTH. During 1934–5 this was the commonest species of the genus in shallow dredgings in Plymouth Sound, especially if stones or Laminaria holdfasts were brought up. It was also found intertidally at Tinside and Millbay West Wharf, and on the floating pontoon at Millbay, and the bathing raft at Tinside. An unusual habitat was the carapace of a *Maia squinado*, dredged in 25 fm. off Rame Head, on which about 40 specimens had built their tubes. *C. acutum* and *C. insidiosum* were often found with this species, but in smaller numbers.

The abundance of this species is the more surprising since it is not present in the rich collections of Corophium made from the same dredging grounds in 1895 1911. It seems possible, therefore, that it is not indigenous at Plymouth. In spite of much enquiry I am unable to find any record from elsewhere, except for the single female from Portugal ; and so I cannot guess at its original locality.

SEX-RATIO AND BREEDING. Of 240 specimens in one collection from Plymouth Sound 99, or 41%, were males. There was no evidence of much seasonal variation in this ratio. Ovigerous females were found in February to December. The proportion of egg-bearing females was high from May to October, but fell off in November and December and was very small in February and March.

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* 1 ♀ in Copenhagen Museum ; Dana Station 4155, 12.6.1930.

VARIATION. The females begin to breed at a length of 3·5 to 4 mm., and attain a length of 5·5 to 6·0 mm. The number of spines on the antennae is more variable than in *C. bonelli* or *C. insidiosum.* The following figures were obtained from 15 ovigerous females :

Antenna I, segment 1, inner edge.	1–3 spines ;	mean 2·5.
,, ,, lower edge.	4–7 ,,	,, 5·3.
Antenna II, segment 4, ,, ,,	4–6 ,,	,, 4·6.

GROWTH CHANGES. In the female the number of spines on the antennae increases with age. In the male the spines on all antennal segments decrease in size, but not apparently in number ; and the degradation is never so complete as in *C. acherusicum* or *C. crassicorne.* Antenna II, segment 4, always remains stout and does not become elongated in the adult males as in these two species.

IDENTIFICATION. The female may be identified from antenna II, segment 4, which cannot be confused except with that of *C. crassicorne.* The large eye and rounded eyelobe will distinguish it from this species.

In the male the shortness and sparseness of the setae on the antennae is characteristic of *C. sextoni* and *C. acherusicum.* In adult males of *C. acherusicum*, however, antenna I has 7–10 segments in the flagellum, and in antenna II, segment 4, is elongate and bears no spines.

26. COROPHIUM TUBERCULATUM Shoemaker.

[Shoemaker, C. R., 1934a, pp. 29–30.]

1905, *C. cylindricum*, Paulmier, Bull. N.Y. State Mus., 91, Zool., 12, p. 167, f. 37 (see above : *C. acherusicum*—Notes on Literature).

DISTRIBUTION. America : Nantucket to S. Carolina.

ECOLOGY. This species is found in oyster-washings, etc., from the mouth of rivers and in harbours.

27. COROPHIUM CALIFORNIANUM Shoemaker.

1934, *C. c.*, Shoemaker, J. Wash. Ac. Sci., 24, No. 8, pp. 359–60, f. 2.

One male specimen only is known, collected from the holdfast of water-logged kelp dredged in 48 fm. in Montery Bay, California.

SECTION C.

Urosome segments fused. Uropods I and II inserted below urosome, not in notches in its lateral margins.

This section contains five species of small or moderate size (2–6 mm.), none of which was known to Stebbing (1906). I have seen all except *C. louisianum* and *C. baconi*. The female of *C. louisianum* is not known, and in *C. simile* antenna II, segment 4, is similar in the sexes. In the remaining three species it is dissimilar. *C. acutum*, *C. lacustre*, and *C. simile* build tubes on hydroids, etc.; the habits of the other two species are unknown. All are marine except for *C. lacustre* which lives in water of a salinity from practically 0·0°/₀₀ to about 15°/₀₀. *C. acutum* and *C. lacustre* are widely distributed.

KEY TO SPECIES.

1.	Margin of urosome consisting of a single convex curve	2
	Margin of urosome consisting of two convex curves, separated by a distinct nick	8
2.	Antenna II, segment 4 with one large curved terminal tooth, and a smaller tooth or lobe above it	3
	Antenna II, segment 4 not so armed	7
3.	Antenna II, segment 5 with no processes on lower margin	4
	Antenna II, segment 5 with distinct processes on lower margin	5
4.	Antenna I, segment 1 with a prominent, forward-pointing angular protuberance near base of inner surface	*C. louisianum* ♂
	Antenna I, not so armed	*C. simile* ♀
5.	Antenna II, segment 5, process long, pointed, near middle of joint	*C. acutum* ♂
	Antenna II, segment 5, process short, blunt, near base of joint	6
6.	Antenna I, segment 1 with 2 spines on lower edge	*C. simile* ♂
	Antenna I, segment 1 with no spines on lower edge	*C. lacustre* ♂
7.	Antenna I, segment 1 with 1 spine: Antenna II, segment 4 with 2 spines; segment 5 with none	*C. lacustre* ♀
	Antenna I, segment 1 with 3 spines: Antenna II, segment 4 with 3 spines; segment 5 with one	*C. acutum* ♀
8.	Antenna II, segment 4 with 3 spines and no teeth	*C. baconi* ♀
	Antenna II, segment 4 with no spines and two terminal teeth, segment 5 with a long hooked terminal tooth on inner margin	*C. baconi* ♂

28. COROPHIUM ACUTUM Chevreux.

[Chevreux, E., 1908, p. 75, f. 6.]

1911, *C. a.*, Chevreux, Mém. Soc. Zool. Fr., 23, p. 271. 1916, *C. acherusicum* (part), Barnard, Ann. S. Afr. Mus., 15, p. 272 (see also *C. acherusicum*). 1925, *C. a.*, Chevreux and Fage, Faune de France, 9, p. 366, f. 359, 374. 1928, *C. a.*, Schellenberg, Trans. Zool. Soc. Lond., XXII, p. 633. 1934, *C. a.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 26, 27.

DISTRIBUTION. Europe: France (R. Lannion, Concarneau), Monaco; England (Plymouth and Studland). Africa: Suez Canal*; Durban.* America: Long Island Sound, Woods Hole, Cape May, Rio de Janeiro. New Zealand: Auckland.*

OCCURRENCE IN ENGLAND. Plymouth, and Studland, Dorset (Dr. J. A. Kitching, coll.). At Plymouth in 1934–5 this species was the commonest Corophium among sponges, coralline Algae and roots of Laminaria near low-water mark on the shores of Plymouth Sound. In these situations it outnumbered *C. sextoni*, *C. bonelli*, and *C. insidiosum*, but in shallow water dredgings (5–20 fm.) it was far less common than *C. sextoni*. In May, 1935, all these species except *C. bonelli* were abundant on the wharfs and pontoon of the Millbay Docks.

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* Specimens examined in British Museum.

ECOLOGY. This species is a tube-builder, intertidally or in shallow water. It haunts harbours and the most saline reaches of estuaries.

SEX-RATIO AND BREEDING. Three collections, of over 100 specimens each, contained 42% and 45% (Plymouth) and 34% (Suez Canal) of males. As in *C. acherusicum*, *C. insidiosum*, and *C. sextoni* males appear to be slightly less common than females.

Egg-bearing females were found in February, March, May, and from July to November. The proportion of females with eggs to those without eggs was higher in the summer than in the winter, though some are probably to be found all the winter through.

29. COROPHIUM LACUSTRE Vanhöffen.

[Vanhöffen, E., 1911, S. B. Ges. Naturf. Fr. Berl., p. 400, f. 1–4, and Sexton, E. W., 1912, Proc. Zool. Soc. Lond., p. 664, pl. 74, f. 13–17.]

1896, *C. crassicorne*, Scherren, Nature, 54, No. 1399, p. 367. 1906, *C. crassicorne* (part), Stebbing, Das Tierreich, 21, p. 691 (" found in Norfolk in almost fresh water "). 1907, *C. grossipes* (part), Gurney, Trans. Norfolk Norw. Nat. Soc., 8, pp. 423, 427 (part), 435 (part), Table II (part). 1917, *C. l.*, Vanhöffen, S. B. Ges. Naturf. Fr. Berl., p. 113, f. 2. 1918, *C. l.*, Hellén, Medd. Soc. Fauna Fl. Fennica, 45, p. 136. 1922, *C. crassicorne*, Tesch, Fl. F. der Zuiderzee, pp. 333–4, f. 6. 1923, *C. l.*, Schlienz, Arch. Hydrobiol. Plankt., 14, p. 429. 1924, *C. l.*, Spandl, S. B. Akad. Wiss. Wien., 133, p. 475. 1926, *C. acutum* var. *chevreuxi*, Poisson and Legueux, Bull. Soc. Zool. Fr., 51, pp. 320–5, f. 5, 6. 1927, *C. l.*, Stephensen, Die Tierwelt der Nord-und Ost-See, 14, X, f., pp. 168–9, f. 40. 1931, *C. l.*, Schijfsma, Tijdschr. Ned. Dierk. Ver., Ser. 3, 2, pp. 168–70. 1934, *C. l.*, Shoemaker, Proc. Biol. Soc. Wash., 47, p. 27.

DISTRIBUTION. Europe: Germany (Frisches Haff, Bremerhaven, Elbe); Finland (Borga); Holland (Zuiderzee); France (Canal de Caen); England (R. Thurne and Heigham Sound, Norfolk). America: Chesapeake Bay to Winyah Bay.

I have compared specimens from Germany (Vanhöffen), France (Le Roux), and America (Shoemaker), with those from Norfolk, and find them indistinguishable.

OCCURRENCE IN ENGLAND. 8.ix.35, River Thurne near Potter Heigham, Norfolk (two collections) and Heigham Sound, found by Mr. G. A. Steven abundantly among *Cordylophora lacustris* and on stems of *Phragmites communis*. The only other Crustacean present was *Gammarus zaddachi*, two specimens of which were present in one collection.

The specimens referred to by Scherren (1896) as *C. crassicorne*, and Gurney (1907) as *C. grossipes* (part), were found in the same localities. Their habits were the same as those of Steven's specimens, and very different from those of *C. crassicorne* or of *C. volutator*, of which *C. grossipes* is a synonym. None of these specimens remain. When they were collected *C. lacustre* was still undescribed, and this is the reason for the misidentification of specimens undoubtedly belonging to this species.

ECOLOGY. *C. lacustre* builds muddy tubes upon submerged plants or animals, especially *Cordylophora lacustris.* It inhabits water of low salinity. Schlienz (1923) states that the species extends in the Elbe from areas where the range of salinity is 0·17 to 0·87 parts of NaCl per thousand, to areas where this range is 0·17 to 20·61. In Norfolk it is known so far only from waters in which there is no tidal effect, but which are kept brackish by a subterranean salt-water table. Gurney (1907) records salinities up to 78 gm. per gallon (1·1 parts NaCl per 1000) in the River Thurne above the tidal reaches.

30. COROPHIUM SIMILE Shoemaker.

1934, *C. s.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 28–9.

DISTRIBUTION. America : Atlantic Coast, S. Carolina to Vineyard Sound, Mass. Found in sponges, or by washing oysters, or scraping piles in sheltered, but not estuarine, water.

31. COROPHIUM LOUISIANUM Shoemaker.

1934, *C. l.*, Shoemaker, Proc. Biol. Soc. Wash., 47, pp. 30–1.

DISTRIBUTION. America : Atlantic Coast, Louisiana, and Missouri (only two specimens known : both ♂♂).

32. COROPHIUM BACONI Shoemaker.

1934, *C. b.*, Shoemaker, Journ. Wash. Sc. Sci., 24, No. 8, pp. 356–9, f. 1.

DISTRIBUTION. America : Pacific Coast, off Peru and Southern California, and in the Behring Sea.

ACKNOWLEDGEMENTS.

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Corophium quadriceps, Dana, 1852, P. Amer. Ac., 2, p. 219; Dana, 1853, 1855, U.S. Expl. Exp., 13 (2), p. 836, pl. 55, f. 8; Bate, 1862, Cat. Brit. Mus., p. 283, pl. 48, f. 7 (copied from Dana 1853–5); Stebbing, 1888, Rep. Voy. Challenger, 29, p. 255; Della Valle, 1893, F. Fl. Neapel, 20, p. 376.

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C. contractum, Stimpson, 1855, P. Ac. Philad., 7, p. 383; Bate, 1862, Cat. Brit. Mus., p. 282; Thomson, 1881*, Trans. Proc. N.Z. Inst., 13, p. 220, pl. 8, f. 9; Thomson and Chilton, 1886*, Trans. Proc. N.Z. Inst., 18, p. 142; Della Valle, 1893, F. Fl. Neapel, 20, p. 374; Hutton, 1904, Index Faun. N.Z. London; Stebbing, 1906, Das Tierreich, 21 (1), p. 692.

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* From internal evidence it seems likely that Chilton (1922), and so also Thomson (1881), and Thomson and Chilton (1886) were referring to *C. acherusicum*. Chilton was unable to distinguish his specimens from Dutch ones of this species lent by Hoek (as *C. crassicorne*); and specimens of *C. acherusicum* from Lyttelton Harbour are in the British Museum.

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APPENDIX I.

List of Specimens Examined of C. bonelli and C. insidiosum.

(a) *C. bonelli*.

Locality and date.		Source of specimens.	Number of ♀♀.
England, Plymouth	1889	British Museum	100
	1908	,, ,,	14
	1895	Marine Biological Association, Plymouth	100
	1905	,, ,,	100
	1907	,, ,,	100
	1911	,, ,,	100
	1934	G. I. Crawford	5
Wales, Tenby	1880	British Museum	1
Colwyn Bay	1898	,, ,,	7
Scotland, Tobermory	1913	,, ,,	6
Loch Swen	1933	Dr. J. A. Kitching	133

Locality and date.		Source of specimens.	Number of ♀♀.
Ireland, Valentia	1896	British Museum	3
Roundstone	1874	,, ,,	50–100
Guernsey	1906	,, ,,	9
France, Portrieux, Grandcamp, St. Vaast		Paris Museum	6
Italy, Naples		Naples Museum	several
Denmark, Lodshusene	1878	Copenhagen Museum	20
,, No locality		,, ,,	50–60
Norway, Oslofjord*		Oslo Museum	68
Haugesund*		,, ,,	17
Bergenfjord*		,, ,,	28
Risør*		,, ,,	29
Bergensfjord		British Museum	1
Trondhjemfjord	1893	,, ,,	32
Solsvig	1908	,, ,,	10
North America, East Coast†		Washington Museum	6
South America, Uschaia‡	1892	Hamburg Museum	11
Picton Is.‡	1892	,, ,,	1
Punta Arenas‡	1892	,, ,,	3
500 miles E.N.E. from Rio de Janeiro	1913	British Museum	1
Falkland Islands	1926	,, ,,	5

In all these collections no ♂♂ were present.

(b) *C. insidiosum.*

Locality and date.		Source of specimens.	Number of ♀♀.	Number of ♂♂.
England, Plymouth :				
Millbay Pontoon	3.viii.34	G. I. Crawford	15	0
,, ,,	3.ix.34	,,	25	7
,, ,,	7.ix.35	,,	9	0
,, W. wharf	8.v.35	,,	94	15
,, inner basin	8.v.35	,,	27	19
Tinside	5.ii.35	,,	2	0
Bull Point buoy	31.v.35	,,	0	1
Neille Point buoy	2.viii.35	,,	2	1
Chelson Meadow	9.viii.35	,,	246	199
Denmark :				
Mariagerfjord, Aamolle	Oct. '22	Copenhagen Museum	8	3
,,	27.v.23	,, ,,	many	5
Frederikshavn	5.viii.23	,, ,,	9	2
,,	13.xii.34	,, ,,	3	2
Östersóen (near Graasten)	Sept. '29	,, ,,	1	1
Germany, Kieler Bucht		Berlin Museum	5	2
Italy, Lake of Venice	Oct. '29§	Prof. A. Brian	100	100
	29.x.35‖		40	40
America :				
Oakland, San Francisco	2.ix.31	Copenhagen Museum	4	3

* Labelled by Sars as *C. bonelli* M. Edw.
† *C. pseudacherusicum*—Shoemaker (1934a).
‡ *C. pseudacherusicum*—Schellenberg (1931).
§ 4,097 ♀♀, 1,244 ♂♂—Brian (1932).
‖ 1,492 ♀♀, 398 ♂♂—Brian in a letter, 1935.

APPENDIX II.

THE BRITISH SPECIES OF COROPHIUM.

Species.	British localities, and habits.
C. volutator (Pallas)	Coasts of Great Britain and Ireland; burrowing in intertidal mud flats, often in estuaries.
C. arenarium n.sp.	Leigh-on-Sea, Essex; burrowing in sand between tide-marks.
C. curvispinum G. O. Sars var. *devium* Wundsch	R. Avon at Tewkesbury; building tubes of mud on weed and stones in fresh water.
C. affine Bruzelius	From Forth and Clyde northwards; burrowing, below low-water mark.
C. crassicorne Bruzelius	Coasts of Great Britain; burrowing in muddy sand from just above low-water mark downwards.
C. bonelli G. O. Sars	Coasts of Great Britain and Ireland; building tubes on weed, etc., from low-water mark downwards.
C. insidiosum n.sp.	Plymouth; building tubes on weed usually in brackish water.
C. acherusicum da Costa	Plymouth, Sheerness, New England Creek (Essex) (formerly, the creek is now shut in and brackish); building tubes on weed, etc., especially on rafts and buoys.
C. sextoni n.sp.	Plymouth; habits as in *C. bonelli*.
C. acutum Chevreux	Plymouth, Studland (Dorset); habits as in *C. bonelli*.
C. lacustre Vanhöffen	R. Thurne and Heigham Sound, Norfolk; building tubes, usually in clumps of *Cordylophora lacustris* in brackish (nearly fresh) water.

Notes on the Distribution of Burrowing Isopoda and Amphipoda in Various Soils on the Sea Bottom near Plymouth.

By

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With 1 Figure in the Text.

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INTRODUCTION.

Preliminary Remarks.

THE earliest detailed account of the nature of the sea bottom near Plymouth is that of Allen (1899), wherein analyses of the soils on the 30 fm. line are coupled with lists of the animals collected by trawl and dredge. Ford (1923) described a number of soils in shallower water, and gave a quantitative list of the bottom fauna, collected with a grab which covered an area of 0·1 sq. m. Smith (1932) described in great detail the soils of the area of shell-gravel which surrounds the Eddystone Lighthouse. By none of these workers, however, was special attention paid to the smaller burrowing Crustacea, which are often overlooked unless they are made the special object of collecting. Some species, e.g. of Bathyporeia and Ampelisca, may be very common, and certainly play an important part in the ecology of the sea-bottom. See Steven (1930) and Hunt (1925).

The object of the present paper is to summarize the results of my collecting of Isopoda and Amphipoda in 1934 and 1935, and to record the nature of the soil in which each species was found. From their small size and the habit of many species of burrowing by ejecting sand grains in a swimming current it seems to me probable that the burrowing Amphipoda, Isopoda, and Cumacea are much influenced in their distribution by the nature of soil. I did not, unfortunately, make precise observations on the Cumacea, or on the Tanaidacea, collected.

Reibisch (1905 and 1906) recorded 87 species of Amphipoda dredged in the North Sea. Many of these were burrowing species, and he recorded the type of bottom from which a number of species were obtained. Zirwas (1911) treated the Isopoda similarly. The distribution of Isopoda and Amphipoda between tidemarks is discussed in a number of papers, among which that of Elmhirst (1931) is outstanding.

The methods of burrowing of *Haustorius arenarius* are described by Dennell (1933), and those of *Talitrus saltator*, *Bathyporeia robertsoni*, *Microprotopus maculatus*, and *Corophium volutator* by Schellenberg (1929).

Collecting Methods.

The collections in Cawsand Bay were made from M.B. *Gammarus*, chiefly with the fine-meshed dredge (Naturalist's pattern) and the D-net. The contents of the dredge (usually about 10 litres) were emptied into a bucket and repeatedly stirred up, the fauna being skimmed off with a flat hand-net of bolting silk, until no more appeared. The contents of the D-net were similarly treated, after the finer particles of sand had been washed out through the mesh. One collection was made with a tow-net towed clear of the bottom behind the shrimp-trawl frame: a sort of ground-rope of loose chain was so fixed as to stir up the fauna of the bottom. As a collecting instrument this was as effective as the D-net, but less convenient to use.

The other collections were made from the S.S. *Salpa* with the fine-meshed dredge (Salpa-pattern). Sometimes a canvas bag was fastened inside the net to avoid washing out of particles of soil of the finer grades: but since the soil was observed to pack very firm in the dredge, and to be washed out very slowly even in rough weather, I think it probable that samples taken from the centre of the mass brought up were in their original condition, and that the loss of soil was not considerable, even when the canvas bag was not used.

The soil brought up was emptied into baths of measured capacity, and an estimate made of its volume. A sample was set aside in a breffit for analysis in the laboratory, and the remainder was sieved through the four "Challenger" sieves. The soil which passed the finest sieve was stirred in water and the smallest specimens collected with a hand-net. In fine weather the resulting collections were probably complete except for very small specimens, or rare species : in rough weather small species must have been frequently missed.

The number of specimens of any species obtained in this way is not a measure of the density of population. The area over which the dredge was worked is not known nor the depth to which it dug, and, owing to the shape of the digging edge, the surface layers of the bottom were collected over a larger area than the deepest layers sampled. It is possible, but I think unlikely, that some species of Amphipoda and Isopoda, as of worms, lie too deep for the dredge to secure them.

For quantitative work a grab would have been necessary, and would have to have been used for repeated observations on the same station over a long period, since the density of animals on the sea-floor is subject to large seasonal and annual fluctuations (Blegvad, 1928). It was not possible to take such an extended set of observations, and considering the further disadvantages of the grab enumerated below, I decided that the fine-meshed dredge was the most suitable instrument for a preliminary survey of the distribution of Amphipoda and Isopoda on various soils. The grab is only effective in calm weather and is not equally effective on all grounds ; for comparing the numbers of animals on diverse grounds it is probably inferior to the dredge. The soils at Plymouth are less suited to the grab than the rather uniform muddy soils chiefly worked by Blegvad (1928) and other Danish workers. Moreover, the instrument available at Plymouth covers only 0·1 sq. m., whereas a 50-litre dredge haul covers 1 sq. m., assuming the mean depth of the digging edge to be 5 cm.

Method of Analysing Soils.

At least 400 c.c. of soil from each station (in stony grounds up to 1000 c.c.) were graded in the sieves standardized by Allen (1899), following precisely the procedure detailed by him on pp. 378–380. By this method eight grades are distinguished.

I. Stones. All inorganic material which will not pass through a 15 mm. sieve.
II. Coarse Gravel. Material left on a 5 mm. sieve.
III. Medium Gravel. Material left on a 2·5 mm. sieve.
IV. Fine Gravel. Material left on a 1·5 mm. sieve.
V. Coarse Sand. Material left on a 1·0 mm. sieve.
VI. Medium Sand. Material left on a 0·5 mm. sieve.
VII. Fine Sand. Material which passes through a 0·5 mm. sieve and, when stirred up with sea-water, settles in 1 minute.
VIII. Silt. Remains in suspension at the end of 1 minute.

The dry-weight of soil of each grade is expressed as a percentage of the total dry-weight of the sample, and these 8 percentages form a record of the nature of the soil, which is comparable with all records similarly obtained. This analysis, particularly for very silty soils, is not so precise as analysis by elutriation methods. It distinguishes, however, between soils which cannot easily be distinguished by inspection.

It should be noted that in soils containing high percentages of fine sand (VII) the mean size of the particles of this grade is much larger in clean grounds (i.e. those with little silt) than in silty grounds. It would, therefore, be misleading to express the nature of such soils by " numerical representations " such as Smith (1932) was able to apply to the Eddystone gravels. Further, in grades I to VI, and perhaps also in grade VII, some of the particles are thin laminae of shell and slate, and others are rounded pebbles. The pebbles in any grade are heavier than the laminar particles, and a pebbly gravel is less suited for small burrowing Crustacea than a shelly gravel, the larger particles of which afford good shelter to Gammarids

Theoretically the eight percentages expressing the nature of the soil are free to assume any values which add up to 100. In practice I found that only certain types of values were assumed, and it is likely that everywhere on the sea-bottom the currents will restrict the freedom of these percentages to assume any value. For example, it is improbable that the percentages of grades I and III will be high, and those of II and IV low. The soils examined by Allen (1899) and by myself can be simply classified as below.

I have arbitrarily defined a simple soil as one having a maximum in one grade, and either no secondary maximum or one of less than 5% : and a mixed soil as one having a secondary (rarely also a tertiary) maximum of over 5% of the whole. A mixed soil may be regarded as formed by the mixture of two (or three) simple soils in proportions only roughly ascertainable from the percentages of the 8 grades. Unless the coarser of these components is present in much greater bulk, the lighter gives character to the soil. For example, a mixture of fine sand and coarse gravel will support a certain number of species usually found in fine sand alone, but not those from coarse gravel alone. The fine sand between the particles of gravel maintains its own character, but by filling in the interstices entirely alters that of the gravel. Most of the mixed soils which I have examined consist of a medium or fine sand with a small mixture of coarse or medium gravel.

The simple soils may be arbitrarily classified as follows :

" mud "—maximum in VIII.
" fine sand with mud "—maximum in VII : VIII >10%.
" fine sand "—maximum in VII : VIII from 2 to 10%.
" fine clean sand "—maximum in VII : VIII <2%.
" medium sand " up to " stone "—maximum in VI up to I.

I have found no soil with a maximum in I, and such a ground would probably be barren. The coarser the soil, the less well defined the maximum.

By this classification the Rame mud grounds are included under "fine sand with mud," but they have a much higher percentage of silt than the soils analysed from Cawsand Bay, and the mean size of fine sand particles is smaller. It is in comparing soils with high percentages of silt that the method adopted here is least satisfactory.

A list of stations and of soil-analyses is given in Appendices I and II. The localities best worked were Cawsand Bay, Whitsand Bay and Bigbury Bay.

BURROWING ISOPODA AND AMPHIPODA.

A list of hauls and of catches of Isopoda and Amphipoda is given in Appendix III (p. 644), with separate lists of burrowing and non-burrowing species. Intertidal collections are not included in these lists but are summarized below.

Between Tidemarks.

Only 11 species of burrowing Isopods and Amphipods were collected from intertidal areas, and in only a few localities (marked with an asterisk) were precise measurements taken of the size of soil particles. In other places an estimate was made of the type of soil.

ISOPODA.

Eurydice pulchra Leach. Drake's Island*, Mothecombe*, Treyarnon (N. Cornwall), Saunton (N. Devon); in fine to coarse sand from about half-tide mark downwards.

AMPHIPODA.

Ampelisca brevicornis (A. Costa). Drake's Island in muddy sand; Salstone in very muddy sand, both at L.W.M.

Bathyporeia pelagica Bate. Trevarrian (N. Cornwall)*, Kynance Cove, Mothecombe*, Wembury*, fine to medium sand, from half-tide mark downwards.

Haustorius arenarius (Slabber). Mothecombe, sand, L.W.M.

Urothoë brevicornis Bate. Drake's Island, sand, L.W.M.

U. grimaldii var. *poseidonis* Reibisch. Salcombe Millbay, fine clean sand*, L.W.M.

Perioculodes longimanus (Bate and Westw.). St. Michael's Mount, Salcombe Millbay, muddy to fine sand, L.W.M.

Pontocrates arenarius (Bate). Wembury*, Dawlish, fine to medium sand from half-tide mark downwards.

P. norvegicus Boeck. Trevarrian (N. Cornwall), Kynance Cove, Mothecombe*, Wembury*, fine to medium sand from half-tide mark downwards.

Guernea coalita (Norman). Drake's Island, shell gravel at L.W.M.

Photis longicaudata (Bate and Westw.). Salstone, muddy soil, at L.W.M.

With the exception of *Eurydice pulchra* and *Urothoë grimaldii* var. *poseidonis* (both of which have been caught below tidemarks by other collectors) these species are all contained in the list of burrowing species collected below low-water mark, and considered in the next section.

Below Low-Water Mark.

The three areas on which my information is most complete are Cawsand Bay, Whitsand Bay, and Bigbury Bay. The soil in Cawsand Bay (St. 2) is fine sand with mud. That in Whitsand Bay (St. 34–39) and Bigbury Bay (St. 43–47, 53, 54) is fine clean sand. I also collected in Bigbury Bay from gravel (St. 50, 51), and fine sand with mud (St. 52), see Fig. 1.

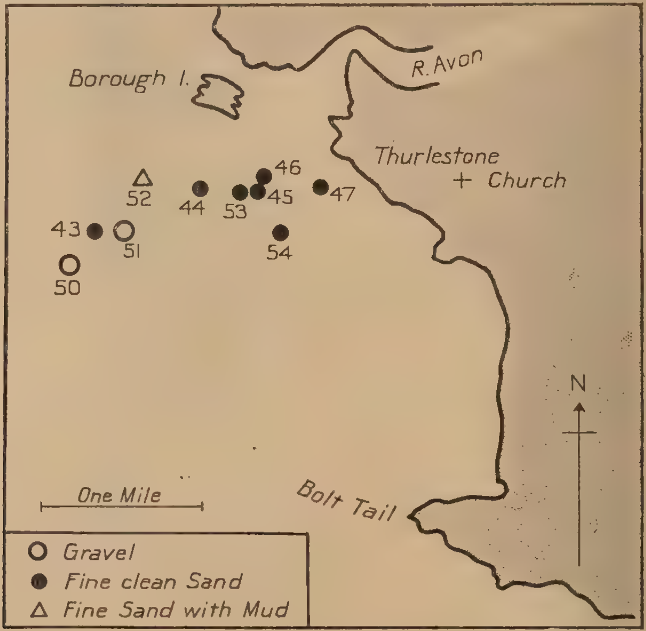

Fig. 1.—Map showing positions of stations in Bigbury Bay, and nature of soil.

A dredge haul from the latter contained *Amphiura filiformis* and *Syndosmya alba*, abundant; *Echinocardium cordatum*, 20 specimens about 1½ inches long; *Cardium echinatum*, 6 large specimens; and a quantity of fragments of oak and hawthorn leaves. The precise numbers of specimens of Isopods and Amphipods caught at these and other stations are noted in Appendix III (p. 644); the following lists simply classify the burrowing species as "abundant," meaning more than 100 in at least one of the hauls, and "few," meaning not more than 10 in any haul. Intermediate frequencies are denoted by "common."

Cawsand Bay (Fine Sand with Mud).

AMPHIPODA.

Ampelisca brevicornis, common.
Bathyporeia pelagica,* few.
Urothoë elegans, few.
Argissa stebbingi, 2 in 7 hauls.
Harpinia antennaria, common.
Perioculodes longimanus, common.
Synchelidium haplocheles, few.
Monoculodes carinatus, 1 in 7 hauls.
Megaluropus agilis, few.
Guernea coalita, 1 in 7 hauls.
Microprotopus maculatus, common.
Siphonoecetes colletti, 1 in 7 hauls.
Corophium crassicorne, common.

The burrowing faunas of the fine clean sand in Whitsand Bay and Bigbury Bay afford an interesting comparison. The soil is very similar, except that that of Bigbury is reddish, while that of Whitsand is greyish-white and composed largely of shell and slate. Some of the hauls in Whitsand contained loose weed, with a fauna of its own, but the presence of weed did not appear to affect the burrowing fauna.

	Whitsand Bay.	*Bigbury Bay.* (Fine clean sand)
ISOPODA.		
Eurydice spinigera,	few.	2 in 7 hauls.
AMPHIPODA.		
Hippomedon denticulatus,	2 in 6 hauls.	4 in 7 hauls.
Ampelisca brevicornis,	—	3 in 7 hauls.
Bathyporeia guilliamsoniana,	few.	few.
B. pelagica,	common.	abundant.
Haustorius arenarius,	1 in 6 hauls.	—
Urothoë brevicornis,	few.	—
Leucothoë sp. indet,	—	2 in 7 hauls.
Perioculodes longimanus,	—	few.
Pontocrates arenarius,	few.	—
P. norvegicus,	—	few.
Synchelidium sp. indet.,	—	few.
Megaluropus agilis,	—	few.
Siphonoecetes dellavallei,	—	few.
Corophium crassicorne,	—	1 in 7 hauls.

The remaining stations are too scattered to form the basis of similar comparisons.

A systematic consideration follows of all burrowing species of Isopoda and Amphipoda collected below low-water mark.

Isopoda.

Eurydice spinigera was present in small numbers in Bigbury Bay and Whitsand Bay in fine clean sand. Two specimens of *E. truncata* were obtained from coarse sand near the Eddystone.

I only found *E. pulchra* between tidemarks. It swam freely in pools on the sands, and in the sea as the tide rose. From this fact, and from the frequency with which species of Eurydice are captured in tow-nets, it appears that they are not so intimately dependent on the soil as are the burrowing Amphipoda. *E. pulchra* burrows with great ease, principally by means of a swimming current.

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* See p. 639

Amphipoda.

Hippomedon denticulatus was never common. It was present in fine clean sand in Whitsand Bay and Bigbury Bay: also in Bigbury at St. 51 in coarse stony gravel (with a little fine sand): and in Eddystone coarse sand.

Ampelisca spp. were very common except in fine clean sand. None were found in Whitsand Bay and only a few *A. brevicornis* in Bigbury Bay. *A. brevicornis* was common in Cawsand Bay, and intertidally at Drake's Island, in fine sand with mud; and in much muddier soil on the Salstone just above low-water mark. It was not found in coarse grounds. The remaining four species were all frequent in mixed soils. *A. spinipes* and *A. typica* were moreover found in gravels, the former more commonly. *A. tenuicornis* was found in mixed soils, and in the very muddy fine sand of the Rame mud, often in large numbers. *A. diadema* was present less commonly in mixed soils.

The burrowing of Ampelisca is not dependent on a flow of water set up by the pleopods, but is performed by the scraping and hauling of the gnathopods, aided by the urosome as soon as it gets a purchase. The fifth and sixth pereiopods are spread out and prevent sand rolling into the hole. In captivity *A. tenuicornis* made a case of sand-grains (not pebbles) loosely aggregated, and indistinguishable from the substratum.

The local Haustoriidae burrow almost entirely by ejecting sand-grains in a powerful swimming current. They do not form tubes. They are pre-eminently inhabitants of sand, and soils containing much clogging silt or many heavy particles are not suitable for them. It is noticeable that the coarseness of the soils inhabited by species of the genus Urothoë is in proportion to the size of adult specimens.

The burrowing of Haustorius is described by Dennell (1933). That of *Urothoë brevicornis* and *U. grimaldii* var. *poseidonis* appeared to me very similar. Burrowing movements were made with the antennae and gnathopods; the third and fourth pereiopods swept off encroaching particles to one side; while the fifth to seventh pereiopods formed a funnel, widest at the hind end, along which the pleopods swept sand-grains in a powerful and diverging current. In their native soil these species burrowed out of sight within five seconds. *Bathyporeia pelagica* from Bigbury Bay could disappear within one second; and some Bathyporeia (sp. indet.) observed in sandy pools near Saunton, N. Devon, entered the sand without any apparent check to their rate of swimming.

Haustorius arenarius was found in fine clean sand in Whitsand Bay, but not in Bigbury Bay. In one unlocalized haul from Whitsand Bay four specimens were obtained. *Bathyporeia pelagica* was abundant and *B. guilliamsoniana* was present in fine clean sand in both Whitsand Bay and Bigbury Bay. *Bathyporeia elegans* Sars is a name applied to a slender form of *B. pelagica* with less well-developed eyes. The specimens of this genus from the finer sand of Cawsand Bay were of this form, but it is doubtful if it is a distinct species.

Of the species of Urothoë obtained the smallest is *U. elegans*, which was found in Cawsand Bay and in silty mixed soils on the Rame–Eddystone Grounds and Melampus, Plymouth Sound. *U. marina*, the largest species, was collected in coarse sand and fine gravel—see also Smith (1932). The two species of intermediate size. *U. grimaldii* var. *poseidonis* and *U. brevicornis*, were both found in fine clean sand, but only very locally, the former at Millbay, Salcombe (intertidally), and the latter on Drake's Island and in Whitsand Bay.

Argissa stebbingi was found in one haul from Cawsand Bay, and in D-net hauls from Middle Sound and Melampus, in rather silty soil (not analysed).

Metaphoxus fultoni was characteristic of gravels, and was even found in the stony gravel of Bigbury Bay (St. 50, where over 95% of Grade I by weight was non-calcareous). The animal is so small that I presume it lives interstitially in the manner described by Nicholls (1935) for certain copepods. *Harpinia antennaria* was only found in grounds that were wholly or predominantly fine sand with mud, and was most common in Cawsand Bay.

A number of specimens of Leucothoë were found in hauls in which all the other species were certainly burrowers. It seems, therefore, that some members of this genus burrow, while others (e.g. *L. spinicarpa*) habitually live among sponges, ascidians, etc. The specimens from Rame mud were *L. lilljeborgi*, the rest could not be named.

The Oedicerosidae do not build tubes, and live principally in sand. They are, however, less restricted in their choice of soils than the Haustoriidae, at least near Plymouth. *Pontocrates arenarius* and *P. norvegicus* were both found in fine clean sand in shallow water or between tidemarks, but never together. *Perioculodes longimanus* was characteristic of the finer Cawsand Bay soil, and was present in Bigbury but not in Whitsand Bay. *Synchelidium haplocheles* was found in Cawsand Bay, and Synchelidium sp. (perhaps *maculatum*) was present in small numbers in Bigbury Bay. *Westwoodilla caecula* was infrequent in mixed soils. Appendix III contains only one record of *Monoculodes carinatus*, and that is from Cawsand Bay; but it appears (Ford, 1923) that gravel is its usual substratum. A specimen that I dredged from shell-gravel on New Grounds was observed, with its scorched brownish colouring, to harmonize closely with that ground. *Eusirus longipes* was only collected from Rame mud.

Of the Gammaridae, *Megaluropus agilis* was common in Cawsand Bay and Bigbury Bay, and is probably a genuine burrower. *Maera othonis* was observed in the laboratory to make a refuge under large shell fragments by pushing out the finer soil with its second gnathopods, creeping on its side, like a Gammarus, when disturbed, and concealing itself under the first suitable fragment found. Since *Cheirocratus sundevalli* and *Ceradocus semiserratus* were found on the same gravelly or mixed grounds, I suppose that their habits are similar.

Guernea coalita is another very small species living in coarse grounds, probably interstitially.

The Photidae and Corophiidae are tube-builders, and a number are burrowers. Of the Photidae only two species were found in numbers, *Microprotopus maculatus* and *Photis longicaudata*, from mixed and simple soils with much fine sand and silt. Of the Corophiidae, *Siphonoecetes dellavallei* was a member of the characteristic fauna of Bigbury Bay, and *Corophium crassicorne* of Cawsand Bay. *S. dellavallei* was also dredged commonly off the bar of the River Yealm in a soil noted as "shelly-slaty fine-gravel," and in small numbers inside Drake's Island. *C. crassicorne* was also obtained off the bar of the Yealm and at White Patches (Zostera bed), and Melampus, Plymouth Sound.

ACKNOWLEDGMENTS.

The success of my collecting trips is practically entirely due to the help and advice of Captain Lord of the S.S. *Salpa*, and to the co-operation of all the crew (especially Mr. J. Martin who did much of the sieving with me). I wish to express my warmest thanks and appreciation to them all.

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APPENDIX I: LIST OF STATIONS.

No. of Station.	Date.	Area.	Marks or Bearings.	Depth (fm.).	Nature of Soil.
2	6.vii.34 (repeated later)	Cawsand Bay	Breakwater light on Bovisand fort: clock tower on highest near bushy-topped tree (2*a* was a sample taken nearby; 2*b* was taken off Pier Cellars).	3–5	Fine sand with mud.
6	18.vii.34	Off Penlee Point	Mewstone on Wembury Church: white house (sea level) on Penlee on 3 tall trees to W. of large wood on Maker Heights.	23	Mixed.
23	14.viii.34	Rame mud	Mewstone open from Yealm Head, on trees on skyline: Penlee Point overlapping Blackball: Rame Chapel on flagstaff.	20	Fine sand with much mud.
24	14.viii.34	Rame mud	Mewstone on head to W. of Yealm: Penlee Point just overlapping Blackball: Rame Chapel on flagstaff. About 300 yd. S.S.E. from last; "Turritella ground."	20–25	As last, but less silty and grittier.
C	14.viii.34	Rame-Eddystone	In a direct line from Rame Head to Eddystone.	28	Mixed soil, chiefly medium sand.
26	4.ix.34	Eddystone	Eddystone bearing S.E. about ¼ mile.	*ca.* 30	Red fine gravel.
27	4.ix.34	Eddystone	Eddystone bearing S.E. by S. about ¼ mile.	*ca.* 30	Pale sandy gravel.
28	4.ix.34	Eddystone	Eddystone bearing S.S.E. about ¼ mile.	*ca.* 30	Pale medium gravel.
32	3.x.34	Rame-Eddystone	Rame Chapel on flagstaff.	27	Mixed soil, chiefly fine sand.
33	3.x.34	Rame Eddystone	Rame Chapel on flagstaff.	25	Fine sand, rather muddy and gravelly.
34	16.xi.34	Whitsand Bay	N.N.E. of Queener Rocks: church just in view at end of haul (going W.).	3–5	Fine clean sand.
35	,,	,,	Opposite wreck of *Chancellor*: Rame Church inside Polhawn house.	3–4	,, ,,
36	,,	,,	¼ mile W. from 35.	3–4	,, ,, (weedy).
37	,,	,,	E. of Shadows Rocks.	3–4	,, ,,
38	,,	,,		3–5	,, ,,
39	,,	,,	Just E. of 34.		,, ,, (weedy).
41	4.xii.34	Plymouth Sound	About 50 yd. N.E. to N. of Melampus buoy: buoy started on Picklecombe Pt., ended on middle of Drake's Is.		Mixed soil (fine sand and coarse gravel).
43	22.i.35	Bigbury Bay	Burgh Is., N.E.: Bolt Tail, S.E.	17	Fine clean sand.
44	,,	,,	Burgh Is., N.: Thurlestone Church, just S. of E.	11	,, ,, (rather red).
45	,,	,,	Burgh Is., N. by W.½W.: Thurlestone Church, E.	7½	,, ,, (red).
46	,,	,,	Burgh Is., N.W. by N.½N.: Thurlestone Church, E. by ½S.	5	,, ,,
47	,,	,,	Burgh Is., N.W.: Thurlestone Church, E.	4¼	,, ,, (red).
50	10.v.35	,,	Burgh Is., N.E.: Bolt Tail, S.E.½E.	19-20	Medium stony gravel.
51	,,	,,	Burgh Is., N.E.½N.: Bolt Tail, S.E.¼S.	18	Coarse stony gravel.
52	,,	,,	Burgh Is., N.E.: Bolt Tail, S.E. by S.	16	Fine sand with mud (leaves of oak, etc.) (= Ford, 1923, Station 13).
53	,,	,,	Burgh Is., N. by W.: Thurlestone Church, E.	9½	Fine clean sand.
54	,,	,,	Burgh Is., N.N.W.: Thurlestone Church, E. by N.	4–5	,, ,,

APPENDIX II: ANALYSES OF SOILS.

Stations in same order as in Appendix III; the maxima are shown in heavy type.

	Fine Sand with Mud.					Fine Sand.									Coarse Sand.	Fine Gravel.	Medium Gravel.		Coarse Gravel.	Mixed Soils.				
Stations.	23	24	2	2*a*	52	34	35	37	39	44	45	47	53	54	27	26	28	50	51	6	C	32	33	41
Grades.																								
I	0·8	1·9	0·1	—	2·3	—	6·4	2·0	1·9	0·3	0·2	—	0·8	1·5	0·4	0·3	1·9	4·6	14·2	4·9	—	1·4	0·6	4·2
II	0·7	3·5	0·2	—		0·1						—			7·2	6·1	13·3	30·9	**28·8**	**7·1**	8·9	**11·8**	7·0	**17·2**
III	1·0	2·3	0·2	0·1		0·2						—			22·5	20·9	**36·5**	**32·6**	15·7	3·8	**10·6**	10·1	**7·2**	6·4
IV	1·8	2·4	0·3	0·1		0·3						—			24·4	**33·1**	28·0	18·8	12·3	3·1	5·8	8·8	5·0	7·1
V	3·7	4·8	0·6	0·4		0·5						—			**27·7**	29·2	13·0	7·0	9·6	6·4	5·8	8·3	4·0	10·2
VI	5·3	6·2	1·0	0·8		4·0	18·6	3·2	4·1		0·5	1·4			12·6	5·5	4·4	2·5	4·4	11·8	**43·9**	19·2	8·7	11·2
VII	**48·8**	**55·3**	**78·4**	**82·7**	**80·8**	**94·7**	**74·6**	**94·2**	**93·8**	**98·5**	**98·4**	**98·2**	**97·4**	**97·7**	4·2	3·9	2·6	2·8	9·6	**52·1**	24·1	**34·7**	**55·5**	**37·4**
VIII	38·0	23·6	19·3	15·7	16·9	0·3	0·3	0·5	0·4	1·3	0·8	0·4	1·8	0·8	1·1	1·7	0·4	0·7	3·2	10·7	1·0	5·8	12·0	6·4

APPENDIX III: FAUNA LISTS.

Type of Ground.	Fine Sand with Mud.											Fine Sand.													Coarse Sand.	Fine Gravel	Medium Gravel.		Coarse Gravel	Mixed Grounds.				
Station No.	23	24	2	2	2	2	2	2	2a	2b	52	34	35	36	37	38	39	43	44	45	46§	47	53	54	27	26	28	50	51	6	C	32	33	41
Instrument‡	F.M.D.†	F.M.D.	F.M.D.	D-net.	D-net.	Tow-net.*	D-net.	D-net.	F.M.D.	D-net.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.*	F.M.D.†	F.M.D.†	F.M.D.	F.M.D.	F.M.D.	F.M.D.	F.M.D.†	F.M.D.	F.M.D.
Approx. Volume in Litres	100	150	–	–	–	–	–	–	–	–	–	70	50	30	30	40	80	30	30	30	40	40	–	–	–	50	–	–	–	–	3	40	30	–
ISOPODA.																																		
(a) *burrowing.*																																		
Cirolanidæ.																																		
Cirolana borealis Lilljeborg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Conilera cylindracea (Montagu)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Eurydice spinigera Hansen	–	–	–	–	–	–	–	–	–	–	–	1	4	1	3	6	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
E. truncata (Norman)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
(b) *in weed.*																																		
Idoteidæ.																																		
Idotea baltica (Pallas)	–	–	–	–	–	–	–	–	–	–	–	c.	f.	–	–	–	c.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I. emarginata (Fabr.)	–	–	–	–	–	–	–	–	–	–	–	o.	f.	–	–	–	c.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
I. linearis (L.)	–	–	–	–	–	–	–	–	–	–	–	c.	f.	–	–	–	c.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Zenobiana prismatica (Risso)	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AMPHIPODA.																																		
(a) *burrowing.*																																		
Lysianassidæ.																																		
Hippomedon denticulatus (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	1	–	–	2	1	1	–	–	–	1	–	–	–	–	–
Ampeliscidæ.																																		
Ampelisca brevicornis (A. Costa)	–	–	23	–	5	2	1	2	2	–	4	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
A. spinipes Boeck	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	6	–	–	1	2	–	3	1	–
A. diadema (A. Costa)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	–	15	20	–
A. tenuicornis Lilljeborg	2	108	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	–	18	24	1
A. typica (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	2	1	4
Ampelisca sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	1	3	3	–	22	–	–	22	83	3
Haustoriidæ.																																		
Bathyporeia guilliamsoniana (Bate)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	3	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
B. pelagica Bate	–	–	7	1	4	6	–	4	1	–	9	1	–	–	2	1	24	386	306	72	7	8	373	517	–	–	–	–	4	–	–	–	–	–
Haustorius arenarius (Slabber)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Urothoë marina (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	1	–	–	–	–	–	–	–	–
U. brevicornis Bate	–	–	–	–	–	–	–	–	–	–	–	4	7	–	3	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
U. elegans Bate	–	–	7	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	19
Argissidæ.																																		
Argissa stebbingi J. Bonnier	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Phoxocephalidæ.																																		
M. fultoni (T. Scott)	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	3	4	2	1	–	–	–	1	–	–
Harpinia autennaria Meinert.	2	3	47	–	2	1	–	4	10	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3
Harpinia sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoidæ.																																		
Leucothoë lilljeborgi Boeck	1	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoë sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	2	1	–	1	–	–	–	1	1	4
Lilljeborgiidæ.																																		
Lilljeborgia brevicornis Lilljeborg	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
Oedicerosidæ.																																		
Perioculodes longimanus (Bate & Westwood)	–	2	37	12	70	37	3	72	8	25	2	–	–	–	–	–	–	5	–	2	–	–	1	2	–	–	–	–	–	–	–	–	–	2
Pontocrates arenarius (Bate)	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P. norvegicus Boeck	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	3	–	1	–	9	–	–	–	–	–	–	–	–	–	–
Synchelidium haplocheles Grube	–	–	–	1	3	–	–	1	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Synchelidium sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	7	1	–	–	–	–	–	–	–	–	–	–
Monoculodes carinatus (Bate)	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Westwoodilla caecula (Bate)	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	3	–
Eusiridæ.																																		
Eusirus longipes Boeck	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gammaridæ.																																		
Cheirocratus sundevalli (Rathke)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	5	–	15
Cheirocratus sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–
Megaluropus agilis Hoek	–	–	–	1	2	2	–	1	–	6	–	–	–	–	–	–	–	–	1	–	–	–	5	9	–	–	–	–	–	–	–	–	–	–
Ceradocus semiserratus (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	17	–	–	–	–	2	1	–
Maera othonis (M.-Edwards)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13	6	3	?1	–	4	–	4	24	2
Dexaminidæ.																																		
Guernea coalita (Norman)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	1	–	–	–	–	–	–	–
Photidæ.																																		
Microprotopus maculatus Norman	–	–	2	16	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Photis longicaudata (Bate and Westwood)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	14	–	2	3	6
Leptocheirus hirsutimanus (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
L. pectinatus Norman	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–
Podoceropsis sophiæ Boeck	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	2	–	1	–	–
Megamphopus sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	–	3
Corophiidæ.																																		
Siphonoecetes colletti Boeck	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. dellavallei Stebbing	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	2	8	–	–	4	6		–	–	–	–	–	–	–	–	–
Corophium crassicorne Bruzelius (b) *in weed.*	–	–	9	6	7	8	–	26	9	4	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–		–	–	–	4
Lyssianassidæ.																																		
Lepidepecreum longicorne (Bate and Westwood)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Socarnes erythrophthalmus D. Robertson	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	?	–
Orchomenella nana (Kröyer)	–	–	–	4	–	7	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leucothoidæ.																																		
Leucothoë spinicarpa (Abilgaard)	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1

* Tow-net dragged about 1 ft. from bottom behind a chain designed to dig up the bottom.
‡ F.M.D.=fine meshed dredge, with (†) or without canvas bag inside, as noted.
c=common.
§ Many specimens lost by tube cracking.
f=few.

	Mud.	Fine Sand with Mud.										Fine Sand.																		Mixed Grounds.				
	23	24	2	2	2	2	2	2	2a	2b	52	34	35	36	37	38	39	43	44	45	46	47	53	54	27	26	28	50	51	6	c	32	33	41
Stenothoidæ.																																		
Stenothoë monoculoides (Montagu)	–	–	1	8	11	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
S. marina (Bate)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Metopidæ.																																		
Parametopa kervillei Chevreux	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Acanthonotozomidæ.																																		
Panoploea minuta	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
Calliopiidæ.																																		
Apherusa bispinosa (Bate)	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
A. ovalipes Norman and Scott	–	–	–	11	26	10	8	16	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Atylidæ.																																		
Nototropis swammerdami (H. Milne-Edwards)	–	–	–	–	–	–	3	1	–	–	–	49	–	1	1	6	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. vedlomensis (Bate)	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
N. falcatus (Metzger)	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nototropis sp.	–	–	–	–	–	–	5	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gammaridæ.																																		
Melita palmata (Montagu)	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
M. obtusata Montagu	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Maera grossimana (Montagu)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
Gammarus locusta (L)	–	–	–	4	1	18	3	4	2	2	–	100	7	10	5	3	57	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
Gammarus sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Dexaminidæ.																																		
Dexamine spinosa (Montagu)	–	–	–	35	43	9	–	5	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aoridæ.																																		
Aora typica Kröyer	–	–	–	38	9	5	–	8	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coremapus versiculatus Norman	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Photidæ.																																		
Eurystheus maculatus (Johnston)	–	–	–	–	1	6	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Amphithoidæ.																																		
Amphithoë vaillanti Lucas	–	–	–	36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Amphithoë sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pleonexes gammaroides Bate	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Jassidæ.																																		
Jassa falcata (Montagu)	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Jassa sp.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Corophiidæ.																																		
Erichthonius brasiliensis (Dana)	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
Corophium sextoni Crawford	–	–	–	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4
C. bonelli G. O. Sars	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
Caprellidæ.																																		
Phthisica marina Slabber	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
Pariambus typicus (Kröyer)	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

The Fauna of Certain Estuaries in West England and South Wales, with Special Reference to the *Tanaidacea, Isopoda* and *Amphipoda.*

By

G. I. Crawford, M.A.,

Assistant-Keeper at the British Museum (Natural History): late Student Probationer at the Plymouth Laboratory.

With 2 Figures in the Text.

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INTRODUCTION.

DURING the summer of 1935 Captain Nicholson of Saltash kindly put his motor-boat at my disposal and took me for seven full-day collecting trips on the estuaries of the Tamar and its confluents, the Tavy and Lynher. I also made some collections from land in the estuaries of the Plym and Exe (S. Devon), Taw (N. Devon), Camel (N. Cornwall), and Towy (S. Wales).

All collecting was done intertidally or in shallow water and was practically confined to the brackish-water reaches. No gear was used except a hand-net of stramin, and a zinc sieve of 1-mm. mesh. More attention was paid to the Crustacean orders Tanaidacea, Isopoda, and Amphipoda than to the rest of the fauna, observations on which were only occasionally made.

No salinity measurements were taken, since Percival (1929) had already recorded enough to give a general impression of salinity-range at various parts of the Tamar estuary, and I had not time for the periodic measurements necessary for a real understanding of the effect of salinity on the distribution of species.

FAUNA OF THE ESTUARIES.

Rivers Tamar, Tavy, and Lynher.

An account of the Tamar and Lynher and their fauna has already been given by Percival (1929). Some of his identifications, as I show on page 656, are probably incorrect.

In the following summary of my collecting the species are arranged in the order adopted in the Plymouth Marine Fauna (1931). The localities are considered in order from the most to the least saline, and the rivers in the order Tamar, Tavy, Lynher. Their position is shown in Fig. 1. For most of the identifications I am entirely responsible. Some specimens of the following species have, however, been examined, and their identification confirmed, by experts to whom I wish here to express my deep gratitude. *Heterotanais örstedii*† was referred to Dr. J. H. Schuurmans Stekhoven of Utrecht; *Cyathura carinata, Idotea viridis,* and *Paragnathia formica* to Professor W. M. Tattersall; *Gammarus duebeni*, *G. zaddachi*, and *G. chevreuxi* to Mrs. Sexton; and *Melita pellucida* and *Leptocheirus pilosus* to Dr. K. Stephensen of Copenhagen.

ISOPODA.

**Cyathura carinata* (Kröyer). Tavy, Mt. Jessop, in mud-flat on river bank: Lynher, Sconner Creek, in mud.

**Paragnathia formica* (Hesse). Tavy, Mt. Jessop, under stone: Lynher, Wivelscombe Lake, Sconner Creek, in "salting cliff."

**Sphaeroma rugicauda* Leach. Tamar, Kingsmill Lake, salting pools; Clifton Marsh, salting pools; Whitsam, open creek; Haye, creek above sluice: Tavy, Mt. Jessop, under stones: Lynher, Sconner Creek, salting pools and cliff; Wivelscombe Lake, salting pools.

**S. hookeri* Leach. Tamar, Crosspark Wood, creek above sluice: Tavy, Lopwell Ford, main channel and creek above sluice.

**Idotea viridis* (Slabber). Tamar, Neille Point, in weed on buoys: Lynher, Wivelscombe Lake, salting pools.

AMPHIPODA.

Melita palmata (Montagu). Tamar, Weston Mill Lake, near H.W.M. among weed; Neille Pt., mussel bed and buoy; Crosspark Wood, among *Obelaria gelatinosa*: Lynher, Rat I., pools and under stones; Wivelscombe Lake, in ditch.

**M. pellucida* G. O. Sars. Tamar, Haye, creek above sluice: Tavy, Blaxton (open) creek, among oak-leaves, etc.; Lopwell Ford, creek above sluice; Lopwell Ferry, main channel under stones.

---

† Kröyer's original spelling of this name was Örstedii: any change beyond altering the capital to a small letter seems to me a breach of Article 19 of the Int. Rules of Zool. Nomenclature.

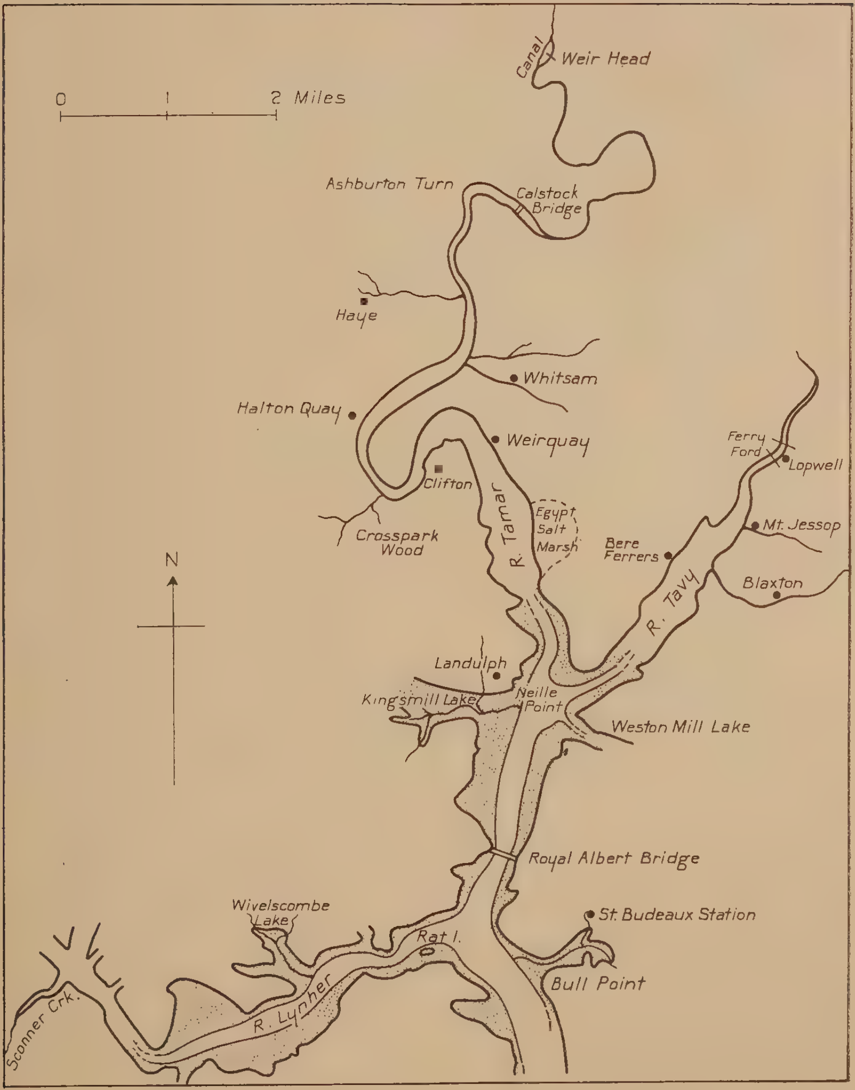
Canal
Weir Head
0 1 2 Miles
Ashburton Turn
Calstock Bridge
Haye
Whitsam
Halton Quay
Weirquay
Ferry Ford
Lopwell
Clifton
R. Tamar
Egypt Salt Marsh
Mt. Jessop
Crosspark Wood
Bere Ferrers
Blaxton
N
R. Tavy
Landulph
Kingsmill Lake
Neille Point
Weston Mill Lake
Royal Albert Bridge
St. Budeaux Station
Wivelscombe Lake
Rat I.
Bull Point
Sconner Crk.
R. Lynher

FIG. 1.—Map of Estuaries of Tamar, Tavy and Lynher.

Gammarus marinus Leach. Tamar, Clifton Marsh, and Crosspark Wood, in Fucus intertidally: Tavy, Blaxton Creek, Fucus at outflow: Lynher, Sconner Creek, Fucus; Rat I., under stones.

G. locusta (L.). Tamar, Bull Pt., buoys; Lynher, Rat I., under stones near L.W.M.

**G. chevreuxi* Sexton. Tamar, St. Budeaux, open creek; Kingsmill Lake, first creek on S. bank, below sluice; Landulph, creek above sluice; Crosspark Wood, creek above sluice; Whitsam, more southerly open creek; Haye, creek above sluice: Tavy, Blaxton Creek, from outflow to nearly fresh water; Mt. Jessop, creek above and below sluice, main channel, and salting pools; Lopwell Ford, creek above and below sluice, main channel; Lopwell Ferry, main channel: Lynher, Sconner Creek, salting pool with *Scirpus maritimus*.

**G. duebeni* Lilljeborg. Tamar, Kingsmill Lake, first creek on S. bank, inside sluice; Clifton Marsh, salting pools; Crosspark Wood, creek above sluice; Whitsam, more southerly open creek: Tavy, Mt. Jessop, and Lopwell Ferry, salting pools.

**G. zaddachi* Sexton. Tamar, St. Budeaux, open creek; Kingsmill Lake, first creek on S. bank, above sluice; Neille Pt., mussel-bed and buoy; Crosspark Wood, among *Obelaria gelatinosa*; Whitsam, more southerly open creek; Haye, creek above sluice: Tavy, Blaxton Creek, from main channel upwards, penetrating into permanently fresh water; Mt. Jessop, creek inside sluice, and main channel; Lopwell Ford, creek outside and inside sluice, main channel; Lopwell Ferry, main channel: Lynher, Sconner Creek, from Fucus.

G. pulex L. Tamar, Weir Head, derelict canal (fresh water).

Orchestia mediterranea A. Costa. Lynher, Rat I., under stones, H.W.M.

O. gammarella (Pallas). Tamar, Clifton Marsh, salting cliff: Lynher, Wivelscombe Lake, above H.W.M.; Sconner Creek, salting cliff.

Hyale nilssoni (Rathke). Tamar, Weston Mill Lake, H.W.M. in weed; Neille Pt., weed on buoys: Lynher, Wivelscombe Lake, among Salicornia and Fucus.

Microdeutopus gryllotalpa A. Costa. Lynher, Wivelscombe Lake, in ditch (J. Nicholson collected these in 1934: I have seen his specimens).

**Leptocheirus pilosus* Zaddach. Tamar, in *Cordylophora lacustris* on rocks, Whitsam and Ashburton turn; on piers, Calstock Bridge.

Jassa falcata (Montagu). Tamar, on buoys, Bull Pt., Neille Pt.

Corophium acherusicum A. Costa. Tamar, on buoys, Bull Pt., Neille Pt.

**C. insidiosum* Crawford. Tamar, on buoys, Bull Pt., Neille Pt.

**C. volutator* (Pallas). In mud: Tamar, Clifton Marsh, in salting pools; Crosspark Wood, creek above sluice; Whitsam, more southerly open creek; Haye, creek above and below sluice; Ashburton Turn and Calstock Bridge, forming tubes in mud aggregated about the stolons of *Cordylophora lacustris*.

INSECTA.

**Aedes detritus* (Halliday). Tamar, Egypt marsh, and Clifton marsh, larvae in salting pools. (J. F. Marshall det.)

MOLLUSCA.

Limapontia capitata (O. F. Müller). Lynher, Wivelscombe Lake, salting pools. (Miss M. V. Lebour det.)

Of these species those marked with an asterisk may be considered the truly brackish-water species, which do not occur normally in fully marine or freshwater conditions. Of the remainder *G. pulex* is a freshwater species (whose presence in Tamar fresh water deserves notice since it is not found in all rivers), and the rest are marine.

From a study of the habitats chosen by the species of Gammarus, it appears to me (as has been remarked by previous workers) that *G. marinus* inhabits a higher tidal level than *G. locusta*, and penetrates farther up the estuary. I can, however, make no general statement about the ecological relationships of the three brackish-water species which would accord with all the facts observed while collecting in this and other estuaries.

The drainage creeks running into these estuaries are usually fitted with a sluice, which is closed by the pressure of the rising tide. Above the sluice the creek is not subject to any considerable influx of salt-water, although the soil may be impregnated with salt, but the level of water rises forming a "freshwater tide." Conditions below these sluices or in "open creeks" are subject to the same fluctuations as those in the main channel.

Two special habitats should be mentioned. (i) The buoys, the weed on which contains a characteristic fauna of which the most noteworthy species are *Corophium acherusicum* and *Jassa falcata*, both marine species. In 267 specimens counted at random from Neille Point buoys there were found :—

Corophium acherusicum	259	*Gammarus zaddachi*	2
C. insidiosum	3	*Melita palmata*	1
Jassa falcata	2		

Idotea viridis and *Hyale nilssoni* were also present.

(ii) The "Salting Cliff," or vertical face where the salt-marsh gives on to the mud-flats. *Paragnathia formica* is found practically nowhere else : *Orchestia gammarella*, *Sphaeroma rugicauda*, and *Carcinus maenas* are present in this and several other habitats.

River Plym.

All collecting from the Plym Estuary was done in the brackish-water ditches of Chelson Meadow on August 9, 1935. These drain by means of a sluice into the estuary of the Plym, at a point where it is practically an arm of the sea. Near the sluice the ditches contain a dense growth of *Ruppia marina*, from which the following species were washed :—

Sphaeroma hookeri, abundant.
Melita palmata, a few.
Leptocheirus pilosus, common.
Corophium insidiosum, abundant.

This fauna persisted in the larger ditches for some distance from the sluice. It was replaced in fresher water by the following :—

Sphaeroma hookeri, abundant.
Gammarus chevreuxi, abundant.
Corophium insidiosum, a few.

These three species penetrated, but not commonly, into water which contained a freshwater flora and insect larvæ.

Gammarus zaddachi was not seen, and only one specimen of *G. duebeni* (in nearly fresh water). On occasions the latter species has been recorded as common, and *Corophium volutator* is known to be present.

River Exe.

Five collections were made in brackish water on July 21, 1935.

1. Countess Wear, bed of main stream under bridge, tidal. *Phragmites communis* on bank, Enteromorpha sp. and *Potamogeton ?pectinatus* in stream.

Gammarus zaddachi abundant, together with several *Limnaea pereger* and a few Asellus sp.

2. Countess Wear, in a tidal ditch to W. of R. Exe.

G. zaddachi, a few.
G. pulex, common.
Succinea putris (Gastropod) and *Haemopis sanguisuga* (Leech) also present.

3. A pond formed behind a sluice on the upper of two streams running through the Powderham Estate. *Scirpus maritimus* and Fucus sp.

Sphaeroma hookeri, 20–30.
Jaera marina, 2.
Gammarus zaddachi, abundant.
Leptocheirus pilosus, 2.
Hydrobia ulvae was also present.

4. Dawlish Warren, stream with freshwater tide, drying out at low water, exposing mud flats. These species, except for *Corophium volutator*, were washed from Fucus and Enteromorpha.

Heterotanais örstedii form *örstedii*, 15 ♂♂, ♀♀ abundant.
Cyathura carinata, 1 (presumably from mud around Fucus roots).
Leptocheirus pilosus, common.
Melita pellucida, several.
Gammarus duebeni, common.
Corophium volutator, common in the mud.

5. The same stream below the sluice.

Leptocheirus pilosus, 1.
Melita palmata, 6.
Gammarus sp., 2.

River Taw (*Caen River*).

On August 4, 1935, several collections were made on the estuary of the Caen River, a confluent of the Taw on its right bank. The results are enumerated below from the mouth upstream, that is in order of descending salinity, with the exception of a few isolated waters which are placed at the end of the section. Their position is shown in Figure 2.

1. Sand at L.W.M., at confluence with R. Taw.

Eurydice pulchra, a few.
Bathyporeia sp. indet., estimated at 4,000 per sq. m.
Haustorius arenarius, a few.

It seems that conditions at this point are nearly marine.

2. Outside sluice of small stream.

Gammarus chevreuxi, 1.

Orchestia ?gammarellus, 3 juv.

3. Salting cliff.

Paragnathia formica, 13.

Sphaeroma ?hookeri, 1.

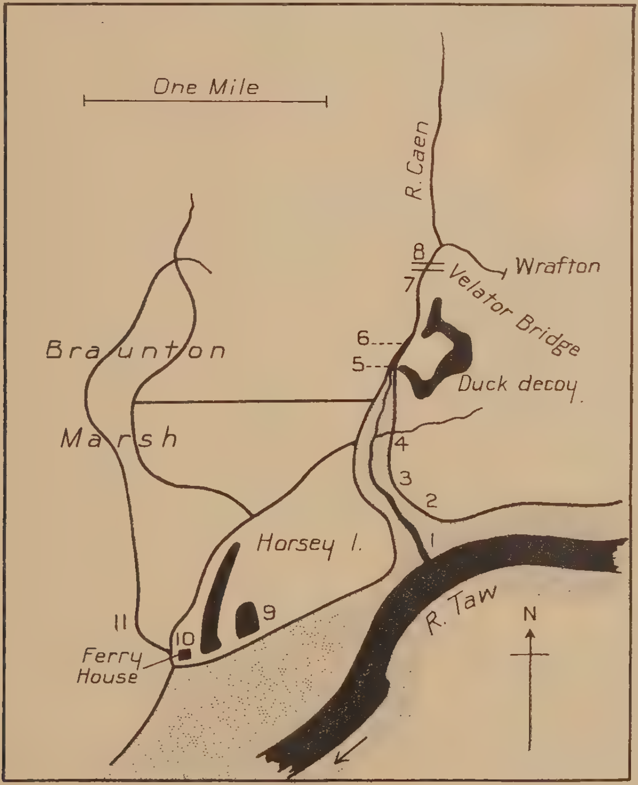
One Mile
R. Caen
8
7
Wrafton
Velator Bridge
6
5
Duck decoy
Braunton
Marsh
4
3
2
1
Horsey I.
R. Taw
N
9
10
11
Ferry
House

FIG. 2.

4. Open stream, above sea-wall.

Cyathura carinata, 1.
Sphaeroma hookeri, 1.
Melita pellucida, a few.

Gammarus chevreuxi, several hundred.
G. duebeni, a few.

4a. The same, below sea-wall.

G. marinus, 9.

G. chevreuxi, 1.

5. S.W. end of Duck Decoy Pond.

G. chevreuxi, 30.
Palaemonetes varians, 3.

Anopheles maculipennis (mosquito), 3 larvæ.
Corixa sp., sticklebacks, water-mites.

This water is presumably nearly fresh.

6. From Fucus at half tide.

Sphaeroma hookeri, 1.
G. marinus, 5.
G. chevreuxi, 3.
G. zaddachi, 2.

7. Channel below Velator Bridge (Enteromorpha and sewage).

G. chevreuxi, about 30.
[*Corophium volutator*, common in mud.]

8. Channel above an 8-ft. sill, just upstream from Velator—entered by tide at extreme high water of spring tides, according to local boys, but probably always fresh.

G. chevreuxi, 50–60.

9. Pond on Horsey I., filled with *Potamogeton pectinatus*. Salinity $10{\cdot}7^{\circ}/_{\circ\circ}$, measured by Dr. L. H. N. Cooper.

G. chevreuxi, common.
Leptocheirus pilosus, abundant on stems, leaves, and especially roots of Potamogeton.

10. Pond on Horsey I.

G. chevreuxi, about 30.
Corophium volutator, about 20.

11. Freshwater ditch.

G. zaddachi, 2.
G. pulex, 9.

G. chevreuxi was by far the commonest of the brackish-water species of Gammarus (though the other two species were both present), and penetrated into completely fresh water.

River Camel.

Collections made on May 5, 1935, opposite Egloshayle Church. This locality appears to be near the upper limit of salt penetration.

Paragnathia formica, common in salting cliff.
Sphaeroma rugicauda, common in salting pools.
Gammarus chevreuxi, a few under stones.
G. zaddachi, several under stones.

River Towy.

Ferryside and Carmarthen are about 7 miles apart: my collecting was done on August 25, 1935, half-way between them, on an extensive salting, intersected by streams coming from high ground to the East. A short distance upstream from this salting, rocky shores came down to L.W.M., near which *Cordylophora lacustris* grew on the rocks. The locality resembled the Tamar between Clifton and Whitsam.

Heterotanais örstedii f. *örstedii*, 1♂, about 20♀♀ in *Cordylophora lacustris*.
Paragnathia formica, 4 in salting cliff.
Sphaeroma hookeri, 2 in salting cliff.
Melita pellucida, 2 among Enteromorpha in open stream.

Gammarus zaddachi, about 30 among grasses, etc., above a sluice; about 20 among Enteromorpha in open stream.
G. duebeni, 15 in hanging grass in open stream.
Orchestia gammarella, 3 in salting cliff.
Leptocheirus pilosus, about 12 in *Cordylophora lacustris*.
Corophium volutator, 5 in salting cliff.

It is surprising that *Heterotanais örstedii*, whose connexion with *Cordylophora lacustris* has been previously noted by Gurney (1907), was not found in the far greater quantities of this hydroid collected from the Tamar. *Gammarus chevreuxi* was specially looked for in the Tavy, and therefore may be presumed to be absent.

BRACKISH-WATER CRUSTACEA IN ENGLAND.

Definition.

It is not possible to define the term "Brackish-Water Species" in terms of salinity, since the changes of salinity to which an animal is subject depend as much on its habits as on the position of its habitat along the estuary. It is possible, however, in the fauna of an estuary to distinguish certain species which belong more properly to fresh water (e.g. *Gammarus pulex*), or to the sea (e.g. *G. locusta*, *G. marinus*, *Melita palmata*, etc.), than to brackish water, although such distinctions are not always clearly marked, and may have only local significance.

If such as these are omitted, there remain 14 brackish-water species of Tanaidacea, Isopoda, and Amphipoda in England, of which I have collected all, except *Corophium lacustre*, from the south-western estuaries.

Literature.

The most important lists of brackish-water Crustacea in Britain are included in the following papers:—

Gurney (1907); Rivers Bure, Yare and Waveney, Norfolk.
Serventy (1935); River Deben, Suffolk.
Omer-Cooper (1916); Christchurch Harbour, Hants (Tanaidacea and Isopoda only).
Percival (1929); Rivers Tamar and Lynher, Devon and Cornwall.

A great number of comparable lists have been compiled for brackish water on the coasts of the Baltic and North Sea. A bibliography of these and a summary of their contents are given by Sick (1933).

Some of these lists contain errors for which I here suggest corrections, either after examining specimens myself, or on the authority of other writers, or (with less assurance) on circumstantial evidence contained in the original paper.

GURNEY (1907). *Gammarus duebeni* refers in part to *G. zaddachi*, Serventy (1935, p. 292). *Microdeutopus* (=*Coremapus*) *versiculatus* on p. 427 and Table II refers to *Leptocheirus pilosus*: I have examined specimens in the British Museum. *Leptocheirus* sp. also refers to *L. pilosus*, Norman (1908). *Corophium grossipes* refers in part to *C. volutator* (pp. 417, 421, 427 part, 435 part, Table II part) and in part to *C. lacustre* (pp. 423, 427 part, 435 part, Table II part). I base this conclusion on circumstantial evidence. *C. volutator* burrows in the mud of estuaries, and *C. lacustre* builds tubes, usually among *Cordylophora lacustris*, in regions of low salinity, and was abundant in collections of this hydroid made for me in Heigham Sound in 1935. *Gnathia maxillaris* refers to *Paragnathia formica*, Monod (1926), and *Heterotanais gurneyi* to *H. örstedii* f. *gurneyi*, Monod (1924).

Serventy (1935). *Heterotanais gurneyi* refers to *H. örstedii* f. *gurneyi*.

Omer-Cooper (1916). *Paragnathia halidaii* refers to *P. formica*, Monod (1926).

Percival (1929). Percival's specimens are not available, and the following corrections are based on what seems to me satisfactory circumstantial evidence. All the species to which I suggest his names apply have been collected by me in the Tamar estuary in localities similar to those which he records. For *Anthura gracilis*, a marine species, read *Cyathura carinata*, a burrower in estuarine mud: for *Sphaeroma serratum* possibly read *S. rugicauda*: for *Idotea baltica* read *I. viridis*, which was common in the Zostera of St. John's Lake: for *Gammarus locusta* read *G. zaddachi*, at least in the less saline parts of its range: for *Corophium crassicorne* read *C. acherusicum*, which was present in the mussel-bed and abundant on the buoys at Neille Point.

Poisson and Remy (1926). Canal de Caen, France. For *Corophium acutum* var. *chevreuxi* read *C. lacustre*. I have examined specimens sent me by Mme Leroux.

Tesch (1922). Zuider Zee, Holland. For *Corophium grossipes* read *C. volutator* (a synonym), and for *C. crassicorne* read *C. lacustre*. Tesch's figures, though crude, seem to refer to *C. lacustre*, and Redeke (1922 and 1932) records *C. lacustre* from the Zuider Zee.

Schlienz (1923). Elbe, Germany. For *Leptocheirus hirsutimanus* read *L. pilosus*. He found his Leptocheirus in *Cordylophora lacustris*, which is the favourite habitat of *L. pilosus*: at Plymouth *L. hirsutimanus* is a marine species.

Table I has been compiled from the papers of Gurney (1907), Serventy (1935), and Omer-Cooper (1916), with such alterations in identification of species as I have suggested. The presence of species in the Tamar is based entirely on my own collecting: the presence of *Corophium volutator* in Chelson Meadow (Plym) is based on the Plymouth Marine Fauna (1931).

TABLE I.

	Norfolk, Gurney (1907).	R. Deben, Serventy (1935).	Christ Church Omer-Cooper (1916).	R. Tamar, etc.	R. Plym.	R. Exe.	R. Taw.	R. Camel.	R. Towy.	Other British Records (list incomplete).
TANAIDACEA.										
Heterotanais örstedii										
f. *örstedii* Kröyer.	—	—	×	—	—	×	—	—	×	
f. *gurneyi* Norman.	×	×	—	—	—	—	—	—	—	
ISOPODA.										
Cyathura carinata (Kröyer).	×	×	×	×	—	×	×		—	
Paragnathia formica (Hesse).	×	×	×	×	—	—	×	×	×	R. Welland (G.I.C.).
Sphaeroma rugicauda Leach.	×	×	—	×	—	—	—	×	—	See Omer-Cooper and Rawson (1934), pp. 34–36.
S. hookeri Leach.	—	—	—	×	×	×	×	—	×	See Omer-Cooper and Rawson (1934), pp. 36–38.
Idotea viridis (Slabber).	×	—	×	×	—	—	—	—	—	
AMPHIPODA.										
Melita pellucida G. O. Sars.	×	—	—	×	—	×	×	—	×	Benfleet, Essex (G.I.C.).
Gammarus chevreuxi, Sexton.	—	—	—	×	×	—	×	×	—	Warwickshire, Pentelow (1931).
G. duebeni, Lilljeborg.	?×	×	—	×	×	×	×	—	×	Essex (G.I.C.). R. Tees, Alexander, etc. (1935)
G. zaddachi, Sexton.	×	×	—	×	—	×	×	×	×	Tewkesbury, Glos; R. Test, Hants; R. Frome, Dorset; Benfleet, Essex (G.I.C.). R. Tay, Bassindale (1933). Essex, Palmer (1933). R. Tees, Alexander, etc. (1935).
Leptocheirus pilosus Zaddach.	×	×	—	×	×	×	×	—	×	
Corophium volutator (Pallas).	×	×	—	×	×	×	×	—	×	Numerous.
C. insidiosum Crawford.	—	—	—	×	×	—	—	—	—	
C. lacustre Vanhöffen.	×	—	—	—	—	—	—	—	—	

Distribution in England.

For all these species, except *Gammarus chevreuxi*, records have been published of occurrences abroad. In Southern England most of them seem to be present in every sizeable estuary. A few do not range over the whole of S. England.

Heterotanais örstedii was not found in England west of the Exe, though in the Tamar and Taw suitable habitats were carefully searched. According to Monod (1924) the two forms *örstedii* and *gurneyi* may live together.

Gammarus chevreuxi was present in the Tamar, Plym, Camel, and Taw, but not in the Towy, Exe, Frome (Dorset), Test (Hants), New England Creek (Essex), or at Benfleet (Essex). Collecting, except in the Frome and Test, was calculated to find this species if present. It is almost certainly absent from the Norfolk rivers and the Deben investigated by Gurney and Serventy. Its presence in inland brackish water near Coventry is well authenticated, Pentelow (1931).

Corophium insidiosum is so far known in England only from the Tamar, Chelson Meadow, and Plymouth Sound. Abroad it has been collected from Denmark, Germany (Kiel Canal), and Italy (Lake of Venice).

C. lacustre is so far known in England only from the Norfolk Broads. It is found abroad in France, Holland, Germany, and North America.

Habitats of Certain Estuarine Species.

Heterotanais örstedii builds tubes on hydroids and weed.

Cyathura carinata burrows in mud. *Paragnathia formica* makes burrows in salting cliffs, but I have found it under stones, cf. Monod (1926). The two species of Sphaeroma are not rigidly attached to one habitat, but live among weed, under stones or in holes in salting cliffs. *S. rugicauda* is especially common in salting pools, and *S. hookeri* in large brackish-water ditches as at Chelson Meadow (Plym). *Idotea viridis* lives on weed, especially on Zostera spp. and Ulva sp.

Melita palmata lives among weed, and is often abundant under stones: *M. pellucida* was chiefly found where there was much decayed land or freshwater vegetation among which it sheltered. The various species of Gammarus shelter among weed, dead leaves or twigs, or under stones.

Orchestia gammarella is found near high-tide mark along sea coasts and estuaries, sheltering under decaying vegetation or stones: it is also found on salt marshes and in holes in the salting cliff. I have found it in fresh water on the cliff near Kynance Cove, 200 ft. above sea-level.

Leptocheirus pilosus builds tubes, especially on *Cordylophora lacustris*, but also on any weed growing in suitable water. *Jassa falcata* builds tubes, especially on buoys.

The species of Corophium build tubes. *C. acherusicum* lives most often on buoys: *C. insidiosum* among weeds in water of rather high salinity (*ca.* $20^{\circ}/_{\circ\circ}$). *C. volutator* builds its tubes in mud, usually on the intertidal mud-flats, or the floor of salting pools or creeks. At Ashburton Turn and Calstock its burrows are made in mud aggregated round the base of *Cordylophora lacustris.* It is frequently found in mud which has settled on horizontal piles. On the Towy I found it in holes in the salting cliff. *C. lacustre* builds tubes on weeds in water of low salinity, especially among *Cordylophora lacustris.*

NOTES ON THE IDENTIFICATION OF GAMMARUS SPECIES.

Seven species of Gammarus are known from England.

G. marinus Leach, marine.
G. locusta (L.), marine.
G. campylops Leach, marine.
G. chevreuxi Sexton, brackish-water.
G. duebeni Lilljeborg, brackish-water.
G. zaddachi Sexton, brackish-water.
G. pulex (L.), freshwater.

I have collected all of these except *G. campylops.* It is probable that there are other species, both marine and estuarine, in Great Britain which are as yet unnamed. Since also the known species are often confused with one another, records should always be critically examined by later workers, if possible with the help of specimens deposited in some trustworthy and accessible institution.

The species about which most confusion has arisen is *G. zaddachi*, which has been frequently recorded as *G. locusta* or *G. duebeni.*

Usually I found *G. zaddachi* easy to distinguish by the criteria listed by Sexton (1912), especially when there were numerous adult specimens available for examination. Younger specimens were not always identifiable unless accompanied by adults. Of these distinctions the most useful is the arrangement of hairs in graduated clusters on the first antenna, and especially on the basal joint; these vary greatly in length from one locality to another, but the general arrangement is characteristic. Other important characters are: (i) hand larger in the second gnathopod than in the first gnathopod, especially in ♂ (in *G. duebeni* the difference in size is slight): (ii) in adult ♂♂ the basal joints of the fifth and sixth pereiopods are only slightly expanded, and the hind corner is free only in the fifth pereiopod. Sexton based her statements on specimens from Bremerhaven, Hamburg, and Ireland. I have found them to be true also for specimens from Devon and Cornwall.

Poulsen (1932) gives a list of features which he states are characteristic of *G. zaddachi*. A number of these were not found in the type material which Mrs. Sexton kindly allowed me to examine, and were not in agreement with statements made in her original description. In particular, Poulsen states that the hind corner of the basal joint of the fifth pereiopod is pointed : I have always found it rounded. Further that the urosome of *G. zaddachi* is not hairy. I have found it always hairy and sometimes, as in the type German material, very hairy. Possibly Poulsen was examining some other species.

Gammarus duebeni is a very stout species, and usually of a muddy greenish- or reddish-brown colour. *G. zaddachi* is more slender, and its colours are more clear. The length and density of the setae on the antennae, limbs, and urosome of *G. duebeni* are very variable, as in *G. zaddachi*, but there are never more than a few small tufts of hairs (not graduated) on the basal joint of the first antenna.

I am not able to distinguish between the habitats of the three brackish-water species, *G. chevreuxi*, *G. duebeni*, and *G. zaddachi*. I found all three in every sort of brackish water in the rivers investigated, and sometimes one and sometimes another penetrated farthest upstream. I found all in fresh water—*G. chevreuxi* in the Taw ; *G. zaddachi* in the Taw (Braunton Marsh), the Tavy (Blaxton Creek), and the Avon at Tewkesbury ; *G. duebeni* up to 200 ft. above sea-level in streams running into the English Channel at Kynance, Cornwall, and nearby, and in similar situations in Anglesey.

There is a great deal of investigation still needed into the systematics, ecology, and physiology of Gammarus, even of the British species.

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A Double-tailed Eulalia.

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With 4 Figures in the Text.

INTRODUCTION.

WHILE examining a bowl of rock dredgings from the Mewstone Grounds near Plymouth, on 10th December, 1926, my attention was attracted by a handsome Phyllodocid worm which had evidently crawled out of a crevice in the broken rocks. On closer investigation the worm proved to be of an unfamiliar species and, of much greater interest, to possess a small secondary tail arising ventrally rather more than two-thirds of the way down the body (Fig. 1). Scale drawings, made at the time from the living animal, have recently been carefully checked by examination of the preserved specimen; only a few slight alterations have been found necessary.

A fairly large number of naturally occurring double-tailed and a few double-headed annelids have previously been recorded, especially among earthworms. A number of other double-tailed or double-headed worms have been produced artificially during regeneration experiments. In nearly every instance, however, the bifurcation is lateral and, with tails especially, very few dorso-ventral bifurcations have been obtained. The worm described in this paper is therefore of considerable interest in that the branching is of the latter type. This bifurcation will be considered first and the specific identity of the worm discussed afterwards.

THE BIFURCATION.

From the head to the 175th segment (the buccal segment carrying the first pair of tentacular cirri is, of course, counted as the first) the worm is perfectly normal. At the posterior ventral border of segment 175 the secondary tail arises. Its first few segments come off almost at right angles to the main body axis, but almost immediately the tail bends back until it is parallel with the primary tail above. In life the secondary tail was generally dragged along below the primary one, but occasionally it would be twisted to the right or to the left as shown in the drawings. It is composed of 28 segments and a pygidium and is about 5 mm. long.

It appears to be a newly grown structure ; its segments are smaller than those of the worm trunk immediately preceding, otherwise they are normally formed. The terminal pygidium has two caudal cirri and an anus.

Viewed from above it will be seen from Figs. 1 and 2 that at the place where the secondary tail arises the main body of the worm perceptibly narrows. The worm is widest about half-way from the head, and for a good many segments before it bifurcates the body width decreases gradually ; this is varied in life by the contractile movements used in crawling. At the fork the main body narrows abruptly owing to the comparatively small size of segments 176 to 179. Succeeding segments are of normal width (except for a slight slenderness of 180, 181 and possibly 182) continuing the interrupted gradual taper of the body to the anus. It should be noted that in Figs. 2 and 3 the normal segments of the primary tail are drawn as shortened, and therefore widened, by longitudinal contraction. The primary tail consists in all of 87 segments.

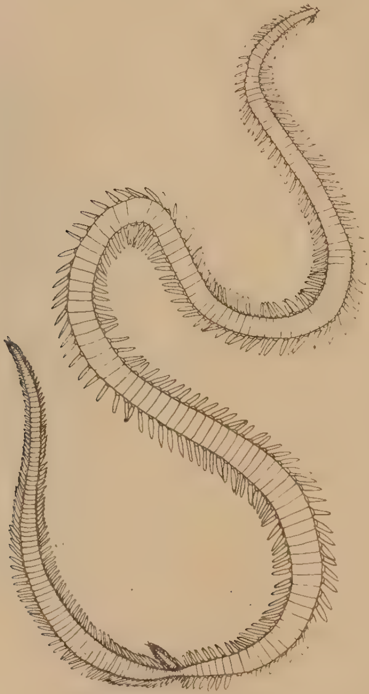
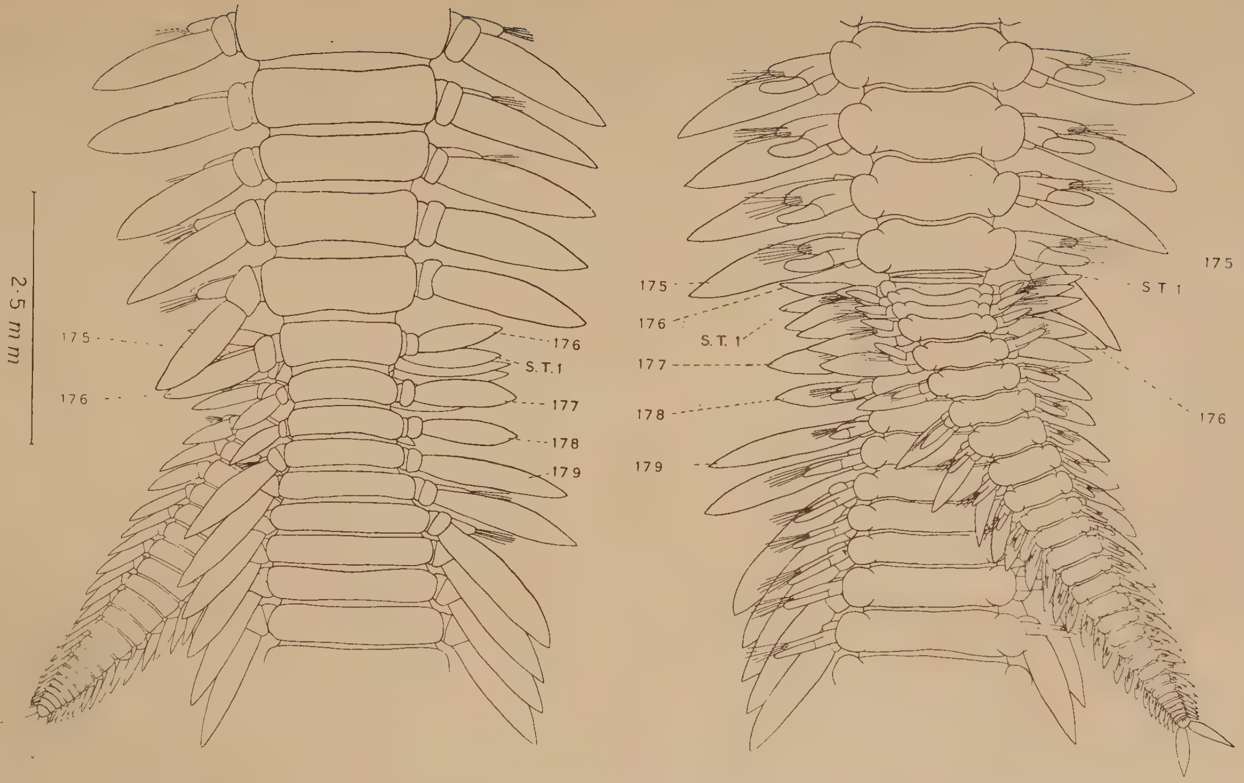


Fig. 1.—Sketch to show general proportions of the worm. From life × 1½ approx.


2·5 mm
175
176
176
S.T.1
177
178
179
175
S T 1
176
175
176
S.T. 1
177
178
179

Figs. 2 and 3.—Dorsal and ventral views of the secondary tail region. Drawn mainly from life. Main body segments 175–179 or their parapodia are numbered. The first segment of the secondary tail or its dorsal cirri are indicated by the lettering S.T. 1.

The parapodial details of the narrowed region provide a clue as to what has happened and will be considered in some detail.

Segment 176. The left parapodium was evidently normal in size or nearly so. Unfortunately it has broken off in the preserved specimen and therefore cannot be checked. The scar can be seen. The right parapodium is smaller than normal, but is complete with bristles and ventral cirrus.

Segment 177. The left parapodium consists only of a very small dorsal cirrus, the other parts of a normal parapodium being absent. The right parapodium, like the one in front of it, is of medium size and is complete with bristles and ventral cirrus.

Segment 178. The left parapodium again consists only of a very small dorsal cirrus, but the right parapodium is of medium size and is complete.

Segment 179. Both parapodia have normal dorsal cirri, but bristle lobes, bristles and ventral cirri are smaller than normal.

On the left ventral sides of segments 178 and 179 the body wall is ruptured. During life a number of eggs, of which the body was full, escaped through the hole, while in the preserved specimen a small portion of the gut protrudes.

Discussion.

There can be little doubt as to how the secondary tail and other abnormal structures came to be formed. It is almost certain that they were due to an injury, perhaps from a fish bite, that had removed a piece of tissue consisting of the ventral body wall of segments 176–179, the left parapodium of segment 176, all the parapodia of segments 177 and 178, and the ventral cirri and bristle lobes of segment 179. With it the nerve cord, together very probably with a ventral portion of the gut as well, would be removed in those four segments. The tail from segment 180 onwards would thus remain attached to the front part of the body only by a strip of dorsal body wall and a portion of the dorsal wall of the gut. For some reason the body did not break finally into two separate portions at this place, as it might very well have done ; instead the wound began to heal. Possibly the left side of the body wall of segments 177 and 178 was cut away at a higher level than on the right side where perhaps only the parapodia had been removed. This would account for the less completely regenerated parapodia on the left where more new tissue had to be formed before they could begin to grow again. It might also be responsible for the hole in the body wall on that side, the gap not yet having closed up. On the other hand the hole may be a new injury in what presumably would be weak new tissue, but I think the first explanation is the more likely.

If the hypothesis just advanced be correct, the appearance of a secondary tail is not at all surprising and might, indeed, have been predicted. We know from the work of others that in annelids regeneration of a new head or a new tail frequently takes place from the cut ends of a worm that has been divided into two portions, although the capacity to regenerate heads and tails varies with the level of the cut and in different species. If this Eulalia had been completely divided by its injury there is no doubt that the anterior portion would have grown a new tail in the ordinary way, and there would then have been nothing abnormal to record. It is merely that the old tail by remaining attached to the anterior portion has complicated the regenerative processes and brought about the formation of a double-tailed monster.

Holmes (1931) and others have demonstrated that in posterior regeneration the presence of the cut end of the ventral nerve cord at wound level is all important if normal regeneration is to follow. In some way the nervous elements govern organization of the new tissues into a properly formed new structure. In an injury such as has been postulated this necessary condition would have been fulfilled and regeneration of a tail would proceed from the region of the cut end of the cord at the anterior border of the wound. That a head did not simultaneously form near the severed nerve cord at the posterior border of the wound scarcely demands explanation, for we know (Berrill, 1928 ; Berrill and Mees, 1936) that in some worms the capacity to regenerate a new head is either confined to the anterior segments or does not exist at all, and Eulalia very likely belongs to one or other of these categories (Okada, 1934, p. 374). In Myxicola, however, Okada (1934) has shown that if the ventral nerve cord be transected artificially, in a manner similar to that which we have supposed to have happened in the present instance, a new head usually appears where the wound is made, generally more readily in the posterior region than in the anterior. In Myxicola it is the capacity to regenerate a tail from such a wound that appears to be almost entirely lacking. Very recently Zhinkin (1936) has produced in the Oligochaete Rhynchelmis secondary ventral tails in the middle of the body by operative removal of a portion of the ventral nerve cord, the operation resembling that of Okada on Myxicola. The artificial wound made by Zhinkin would be closely similar to the natural wound in my Eulalia. Incidentally Morgan many years before had supposed (1902, p. 372) that a double-tailed worm would result from such a mutilation.

I do not propose to mention individually the fairly numerous double-tailed worms with lateral bifurcation which have been described. A good bibliography of these can be found in Leloup (1931). In them it is the rule for the ventral nerve cord, and often the gut also, to fork and to pass into both branches of the worm. Dorso-ventral bifurcation, on the other hand, has rarely been seen, especially in naturally occurring examples, but

Andrews (1894) has described a number of bifid specimens of this type, all of the same species, *Podarke obscura*. They are closely comparable with my Eulalia. In them the intestine divided and passed into both branches, but the ventral nerve cord passed from the main anterior trunk into the ventral branch only. The dorsal branch contained its own ventral nerve cord which ended abruptly at the place where the bifurcation took place. Andrews came to the conclusion that the dorsal branch was the original tail of the worm and that the ventral branch was a new structure formed after injury to the ventral nerve cord. His operative experiments made in an attempt to prove this gave negative results. As we have seen Zhinkin has since been successful in an Oligochaete.

In my specimen the internal anatomy cannot be definitely determined without sectioning and I have preferred to keep the specimen intact. There can be little doubt, however, that it is closely similar to what Andrews found in Podarke, and this conclusion is supported by the results of stimulation experiments made on the worm while it was alive. By work on an annelid Bailey (1930) has shown that " impulses for locomotor movements travel only in the ventral nerve cord " and that a cut through the cord stops the passage of a contraction wave down the body. On this principle it is possible to test for places of interruption in the cord. When the primary tail of the Eulalia was anywhere stimulated with a needle the whole of it would contract, but the wave of contraction did not pass forwards beyond the bifurcation or into the secondary tail. Stimulation of the latter structure brought about a contraction that spread into the worm body anterior to the place of forking, but which did not affect the primary tail. Stimulation of the worm anterior to the bifurcation caused a contraction that did not spread to the primary tail. From these observations it seems a reasonably safe conclusion that the ventral nerve cord of the anterior part of the body is continued into the secondary tail, and that the cord of the primary tail is isolated from the rest of the worm. This agrees with the arrangement in Andrews' specimens of Podarke and with his similar stimulation experiments. Incidentally his paper was not seen by me until after my worm had been preserved.

The arrangement of the gut in my Eulalia is not known, but very probably it bifurcates and supplies both tails, each of which has an anus. Faeces can be seen inside that portion of the gut which protrudes in segments 178 and 179.

Finally it may be advisable to mention that although McIntosh gives a figure (1908, Plate XLIX, Fig. 1) which appears at first sight to represent a *Phyllodoce lamelligera* Linn. bearing a secondary tail essentially similar to that of my Eulalia, I consider this figure to be merely an unfinished drawing of a normal worm. In his text McIntosh says nothing whatever about the peculiar position in which the tail is represented. Okada

(1934, p. 374), however, seems inclined to interpret the figure as that of a worm with a secondary tail. If Okada were now to substitute my record for this very doubtful one from McIntosh his argument would still hold good.

The Specific Identity of the Worm.

The specific identity of the worm is puzzling. It definitely belongs to the genus Eulalia, but I have not been able to decide as to the species. It is quite unlike any Eulalia I have seen during ten years of watching and I cannot satisfy myself that it agrees with the published description of any species. At the same time I am reluctant to propose a new species on the basis of this single specimen, already abnormal in part ; indeed, I do not consider such a course advisable in the present unsatisfactory state of the systematics of the genus itself. The worm would not have been mentioned but for the interest aroused by its secondary tail, and I therefore do not feel called upon to do more than to give a full description of it, leaving its status to be decided on some future occasion.

In the preserved and somewhat contracted condition the worm measures about 13 cm. long with a maximum width (excluding the feet) of about 2 mm. There are 262 segments between head and pygidium, 4 of which are abnormal where the secondary tail of 28 segments arises. The body tapers towards both ends.

The prostomium is well rounded, being broader than long. In the preserved condition the anterior portion bearing the tentacles is more distinctly constricted off from the posterior portion by a transverse groove than it was during life. Four of the five tentacles are relatively long, but the fifth or median tentacle appears as though the tip had been cut off accidentally. This tentacle is set level with the front of the eyes. The eyes are large, brown-black in colour.

The first segment bears a pair of tentacular cirri ; their proportions are indicated in Figure 4. The dorsal tentacular cirri of the second segment are very long ; the ventral cirri are shorter and rather flattened. The fourth pair of tentacular cirri are nearly as long as the preceding dorsal cirri. In the preserved specimen all cirri are somewhat contracted. In Bergstrom's formula the tentacular segments are expressed as follows :—

$$1+\mathrm{O}\frac{\mathrm{ol}}{\mathrm{a1}}+\mathrm{B}\frac{\mathrm{ol}}{\mathrm{aN}}$$

This is based on a dissection of the left side where bristles cannot be seen on the second segment, but it is just possible they have fallen out. Bristles cannot be seen on the right side of this segment either, but as this side has not been dissected it is more difficult to be certain that none is present.

The parapodia vary little from one end of the body to the other. The dorsal cirri are large, leaf-like and pointed. The bluntly rounded ventral cirri do not project beyond the end of the bristle lobe, at least in the preserved state. The bristle lobe has well-rounded lips.

The bristles have swollen denticulate ends to their shafts. On each side one tooth is more prominent than the others. The slender curved blade is finely toothed along its inner edge.

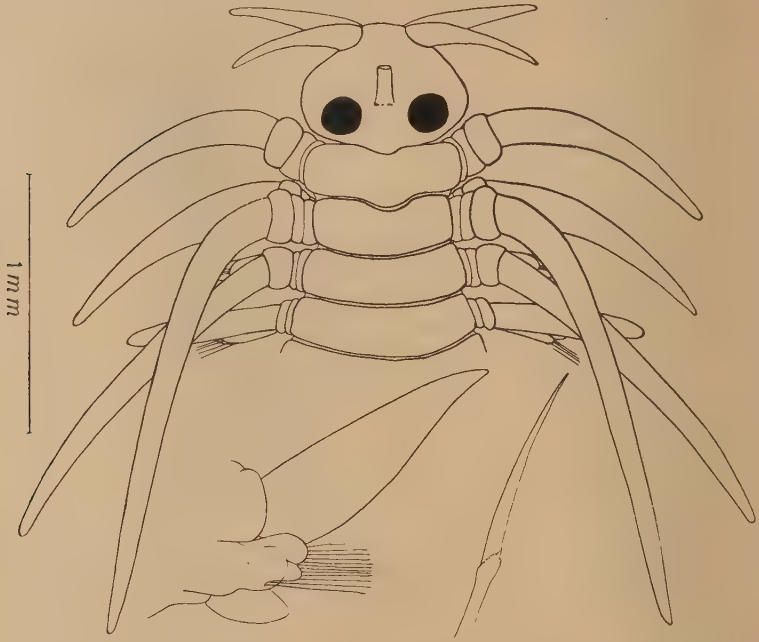


FIG. 4.—Head of the double-tailed Eulalia, from life. The scale is given alongside. Below are drawn an eighty-second parapodium × 25 approx. and one of its bristles × 310 approx. after mounting in Farrant's Medium.

The tiny pygidium carries two large anal cirri similar to those on the secondary tail (Figs. 2 and 3).

The proboscis is, unfortunately, not everted.

In life the prostomium, tentacles and tentacular cirri were yellow. The dorsal surface of the body anteriorly was brownish yellow changing to green farther back, to become rapidly yellow again in the last thirty segments. The green colour was due to the body being filled with large numbers of green eggs underlying the yellowish skin. The inter-segmental folds were blue-green, giving a transversely barred effect. An ill-defined dusky band ran down the mid-dorsal surface from the head ; it gradually became lighter than the surrounding colours and continued to the tail as a faint band of lighter shading. The dorsal cirri were bright yellow, sometimes with a green tinge and with a few brown specks on most of them. The bristle lobes and ventral cirri had also one or two brown spots, and a few were present on the sides of many segments close to the insertions of the parapodia. Ventrally the colour was similar to that dorsally, except that two dark blue-green bands ran along on each side of the middle line over the greater length of the body.

The colour pattern of the secondary tail resembled that of the main body. It was greenish near its insertion, owing to contained eggs, but turned to yellow towards its extremity.

The preserved specimen (in alcohol) is very pale pinkish brown. The dark brown spots mentioned above can be seen.

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"Organic" Phosphorus in Sea Water from the English Channel.

By
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The amount of phosphorus in sea-water in organic combination has in recent years received considerable attention. For its determination various methods have been proposed of which the most promising is that of Kalle (1935). The writer has examined a method in which sea-water was evaporated in a platinum dish with sulphuric acid to remove halides, the resultant melt being dissolved in water and treated successively with permanganate and sulphite, made up to a known volume and its phosphorus content determined colorimetrically. This method promised well as a reference method by which others could be checked, but it was very tedious particularly as only a limited amount of platinum ware was available. As a routine method Kalle's modification of Winkler's procedure is much more promising but here it has not given results as concordant as could be wished, the main source of error being a rather large reagent blank which it has not proved possible to reduce. The total content of phosphorus and arsenic, calculated as phosphorus, as found by Kalle's method, appears to be somewhat less than by the evaporation-permanganate oxidation method. One sample gave 1·20 mg.-atom by the permanganate method and 1·00 mg.-atom per cubic metre by Kalle's. This suggests that there may be incomplete oxidation either of arsenite or of organic phosphorus compounds. When a solution of Waksman's ferri-ligno-protein complex (which may well be typical of some of the more resistant organic constituents of sea-water) was added to sea-water, so as to give 120 mg./m^3 of added iron, and then oxidized by bromine water as in the method for "total iron" (Cooper, 1935), only 40% of this iron was set free. It would thus appear that any practicable method of oxidizing organic material in sea-water without prior evaporation is likely to be incomplete. Nevertheless the possibility that iron or phosphorus, that cannot be set free by such drastic processes, has any immediate biological value is remote, so that Kalle's method may quite well give a figure for total biologically available phosphorus (+arsenic).

To reduce arsenate to arsenite and so to render the colorimetric determination of phosphorus free from interference by arsenic, Kalle advocates thiourea. In trial experiments with known amounts of arsenic *in concentrations likely to be found in sea-water* the writer has been unable to effect any reduction whatever with thiourea, with bisulphite, with "Analytical Reagent" zinc or with a special activated zinc containing small percentages of cadmium, copper and tin. Dr. Kalle has very kindly supplied a sample of his own thiourea, but no better success was achieved with this. At high dilutions complete reduction of arsenate to arsenite and the converse oxidation are known to be difficult to bring about and to be very dependent upon the pH value of the solution. The precise conditions for the reduction, which Kalle has evidently found, are difficult to reproduce and investigators intending accurately to determine total phosphorus should make certain that they have succeeded in removing arsenic present.

The conditions governing the arsenate-arsenite equilibrium in sea-water may themselves be of biological interest since to a limited extent for a limited range of species arsenic is able to replace phosphorus (cf. Atkins and Wilson, 1927).

In Table I are given analyses of total phosphorus+arsenic, $\Sigma(P+As)$, in samples of sea-water either unfiltered or filtered through Schleicher and Schüll's filter paper No. 589 (Blueband) as recommended by Kalle. Judging from subsequent work in this laboratory on iron, a membrane filter ought to prove more efficient. The organic phosphorus+arsenic content of unfiltered water from Stations E1 and L4 in early spring and July appears to be very constant. The arithmetic mean of all determinations is 0·44 mg.-atom/m.^{3} and it is of interest that the arithmetic mean of all Bôto's determinations (1935) of organic phosphorus by Kalle's method off the coast west and south of Portugal between the surface and fifty metres in August and September, 1934, average 0·30 mg.-atom/m.^{3} and that the arithmetic mean of Seiwell's results (1934) between the surface and fifty metres for thirteen stations in the Western North Atlantic in February and March averaged 0·46 mg.-atom. Kreps and Osadchih (1933) by a somewhat different method found in the Barents Sea an annual mean of only 0·24 mg.-atom organic phosphorus (including arsenic) per cubic metre. An examination of all the records shows that organic phosphorus+arsenic in the surface layers of the North Atlantic averages about 0·4 mg.-atom per cubic metre. Around Iceland with an earlier provisional method, Kalle (1933) found values for the surface which were all consistently much higher, averaging 1·1 mg.-atom/m.^{3} In an interesting set of analyses by his present method for a September station in the North Sea he found (mg.-atom/m.^{3}) :—

PO_4–P.	ΣP in unfiltered water.	ΣP in filtered water.	Org. P in unfiltered water.	Org. P in filtered water.
0·17	0·89	0·53	0·72	0·36

Arsenic was said to have been removed by thiourea.

Off Plymouth in July, 1935, results were also obtained on filtered water, but the two sets of analyses cannot be regarded as conclusive. Work here in 1934 had shown that seldom was more than 0·03 mg.-atom P/m.^{3} present as plankton caught in a silk net with 200 meshes to the linear inch, while Harvey's investigations have also shown that nannoplankton able to pass such a net was unlikely to be present in such bulk as to equal the net catch. The origin of such a large organic phosphorus fraction removable by filtration through filter paper is therefore still unknown.

Rakestraw and Lutz (1933) carried out direct determinations of arsenic on the waters in the neighbourhood of Woods Hole; the arithmetic mean of all their results from the surface down to fifty metres was 0·19 mg.-atom per cubic metre. Again, in waters from seventy metres in the English Channel in November, 1921, the Government Chemist found 0·25 mg.-atom/m.^{3} (Orton, 1924). Thus about 0·2 mg.-atom/m.^{3} arsenic is present in sea-water, probably mostly as arsenite, which after oxidation in any of the methods used for determining total and organic phosphorus should yield arsenate which behaves like an equivalent amount of phosphate in colorimetric determinations.

The inference is therefore that at least one-half of the so-called organic phosphorus is really arsenite (cf. Atkins and Wilson, 1927) and that the quantities of phosphorus in organic combination present in the surface layers of the Atlantic are not in general such as to play any large part in the food chain in the sea.

The measurements of " organic phosphorus " by Kreps and Osadchih (1933) and by Seiwell and Seiwell (1934) evidently include arsenic since no steps were taken to remove it.

SUMMARY.

Determinations of organic phosphorus (so called) have been made in waters from off Plymouth. The amount varies little with the time of year and averages 0·44 mg.-atom per cubic metre. This is of the same order as determinations in other parts of the North Atlantic. About one-half of this " organic phosphorus " is considered really to be arsenite.

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TABLE I.

TOTAL AND ORGANIC PHOSPHORUS (INCLUDING ARSENIC CALCULATED AS PHOSPHORUS).

MILLIGRAM-ATOMS PHOSPHORUS PER CUBIC METRE.

Date.	Station.	Depth m.	PO_4–P.	Analyses on unfiltered water.		Analyses on filtered water.	
				$\Sigma(P+As)$	Org. $P+As$	$\Sigma(P+As)$	Org. $P+As$
12-ii-34*	L4	0 & 25‡	0·39	0·84	0·45	—	—
	E1	0, 5 & 50‡	0·32	0·64	0·32	—	—
26-ii-35†	L4	0	0·39	0·79	0·40	—	—
		25	0·42	0·86	0·44	—	—
		45	0·42	0·87	0·45	—	—
		Average§	*0·41*	*0·84*	*0·43*	—	—
	E1	0	0·42	0·82	0·40	—	—
22-iii-35†	L4	0	0·37	0·77	0·40	—	—
		5	0·32	0·84	0·52	—	—
		25	0·39	0·79	0·40	—	—
		45	0·39	0·79	0·40	—	—
		Average	*0·37*	*0·80*	*0·43*	—	—
	E1	0	0·52	0·97	0·45	—	—
		5	0·37	0·81	0·44	—	—
		50	0·35	0·87	0·52	—	—
		67	0·35	1·10	0·75	—	—
		Average	*0·36*	*0·88*	*0·52*	—	—
4-vii-35†	L4	0	0·04	0·42	0·38	0·14	0·10
		5	0·02	0·58	0·56	0·29	0·27
		25	0·17	0·53	0·36	0·50	0·33
		45	0·20	0·53	0·33	0·50	0·30
		Average	*0·13*	*0·53*	*0·40*	*0·45*	*0·29*
	E1	0	0·07	—	—	0·30	0·23
		5	0·05	—	—	0·35	0·30
		15	0·07	—	—	0·30	0·23
		25	0·12	—	—	0·48	0·36
		50	0·22	—	—	0·81	0·59
		Average	*0·16*	—	—	*0·59*	*0·43*

* Analyses on 12-ii-34 by evaporation—permanganate oxidation method.
† Analyses in 1935 by Winkler-Kalle method.
‡ Mixed sample from depths stated.
§ Average content of water column; for definition and method of computation see J. Mar. Biol. Assoc., N.S., 1933, Vol. 18, p. 722.

The Seasonal Abundance of the Pelagic Young of Teleostean Fishes in the Plymouth Area. Part IV. The Year 1936, with Notes on the Conditions as shown by the Occurrence of Plankton Indicators.

By

F. S. Russell,

Naturalist at the Plymouth Laboratory.

With 4 Figures in the Text.

In continuation of the three previous reports on the seasonal abundance of the pelagic young of teleostean fishes (Russell, 1930, 1935 and 1936) the corresponding data for the year 1936 can now be given. These are published in the same form as in the previous reports to which reference should be made. The dates on which the collections were taken are given in Table I and the monthly average catches for the young fish in Table II. No observations were available between October 12th and December 16th, but this does not materially affect comparison with other years because normally the young fish present at that time of year are very few in number. As in previous years the results are based on half-hour oblique hauls with the 2-metre ring-trawl. In Fig. 1 is given the curve for the average catches for each fortnight for all young fish, excluding Clupeids, and superimposed upon this the corresponding curve for the average of the period 1930 to 1934 inclusive (see 1935, Fig. 1).

Two features are at once noticeable in this figure for 1936; first, the almost complete absence of the usual peak of the young of spring spawners, and second, the increase in the numbers of the young of summer spawners as compared with those in the years 1934 and 1935. The sum of the monthly average catches of those post-larvae which show maximal abundance in the months June to October inclusive (see 1935, Table II), excluding Clupeids, was 115 in 1936, as against 79 in 1934 and 37 in 1935.

Below are given for the more important species the sums of the average monthly catches for the year 1936 divided by the corresponding average sums for the period 1930 to 1934 (see 1936, p. 601). In the second column are given the figures for the best year divided by the worst year in the period 1930 to 1936 inclusive.

	1936/Av. / 1930–34.	Best / / Worst.
G. merlangus	0·07	23·6 (1932/1936)
G. minutus	0·07	40·3 (1931/1935 & 36)
Onos spp.	0·62	13·0 (1930/1935)
Arnoglossus spp.	0·24	11·5 (1931/1934)
S. norvegicus	0·32	5·4 (1932/1935)
P. limanda	0·33	14·0 (1931/1935)
P. microcephalus	0·13	20·5 (1932/1935)
S. variegata	0·27	5·9 (1932/1936)
Callionymus spp.	0·31	3·4 (1930/1936)
S. scombrus	0·59	11·2 (1930/1935)
Gobiid spp.	0·47	39·7 (1930/1935)

The year 1936 has thus been the worst year recorded for the period 1930 to 1936 for *G. merlangus*, *S. variegata* and Callionymus spp.* For *G. merlangus* the best year, 1932, was 23·6 times greater than 1936.

The phosphorus available at the beginning of the year 1936 was still low, deviating −11% from the mean content for the winters 1923–24 to 1934–35 (data kindly supplied by Dr. L. H. N. Cooper).

Figs. 2 and 3 give the data on the occurrence of plankton indicators at Plymouth in 1936 in continuation of those given in the last report (1936, p. 599, Figs. 2, 3). Fig. 2 shows that until August in 1936 there was a distinct preponderance of *Sagitta elegans* over *S. setosa*. This is, however, in no way comparable with the predominance of *S. elegans* in 1930 since the upper half of this figure shows that its numbers were very low. Accompanying *S. elegans* there have also been a few of its associated indicators, e.g. Aglantha, Euphausian larvae, and *Themisto gracilipes* (see Fig. 3). *S. setosa* occurred in fair numbers temporarily in February during a period of strong easterly gales. A remarkable feature of the year 1936 has been the return of the siphonophore, *Muggiaea atlantica*. This species disappeared after the year 1924 and was replaced thereafter by *M. kochi* (Russell, 1934). In 1936 *M. kochi* did not appear after January. There have been indications of the occurrence of oceanic water. On March 16th Dr. M. V. Lebour gave me a medusa from the plankton which, while not identifiable for certain, was most likely a young stage of the Laodiceid, *Chromatonema rubra*. This is a deep-sea medusa. On March 26th and 31st specimens of the oceanic scyphomedusa Pelagia also appeared in the ring-trawl collections. It is interesting to note that these animals appeared immediately after the sudden decrease of *S. elegans* in March. This appearance of oceanic animals together with the occurrence

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* In the corresponding table for 1935 (see 1936, p. 601) Callionymus spp. 0·20 should read 0·34 ; the average for the period 1924–29 had been used in error instead of that for 1930–34.

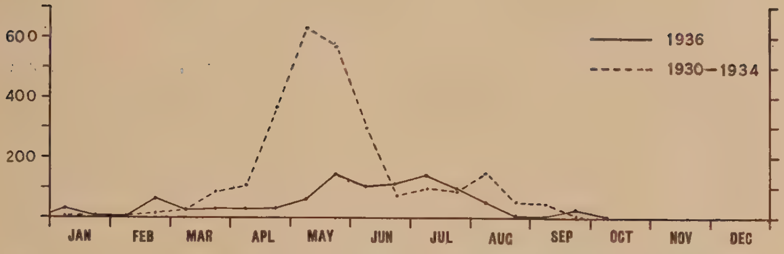

Fig. 1.—Curves showing the average catches in half-hour oblique hauls with the 2-metre ring-trawl for each fortnight for all young fish, excluding Clupeids, in 1936 (————) and the same averaged over the period 1930 to 1934 inclusive (– – – –).

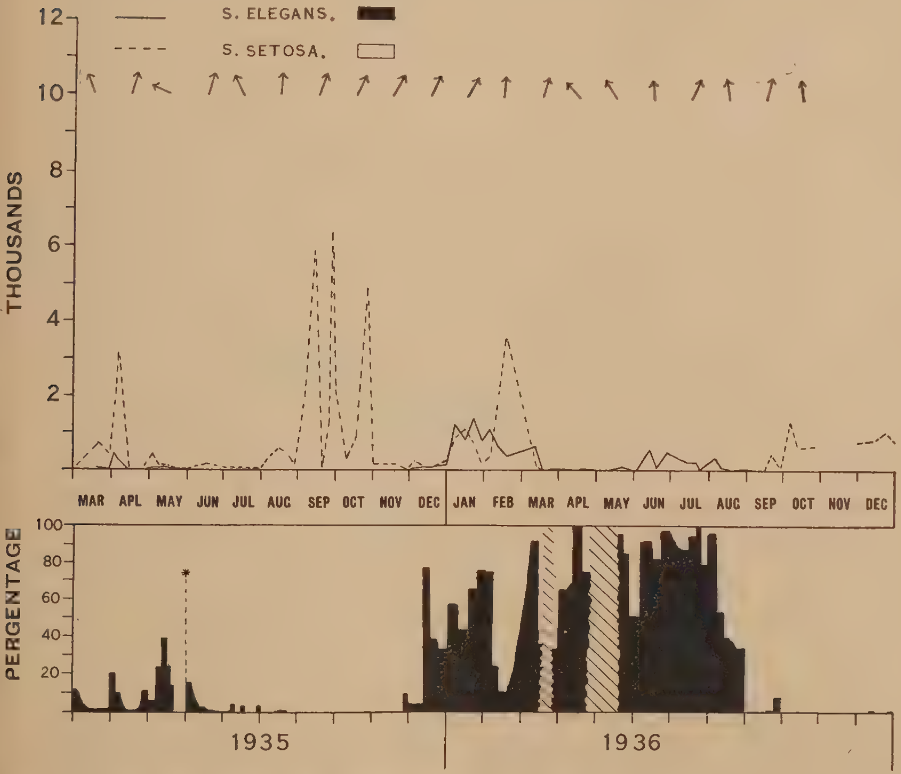

Fig. 2.—Above, curves showing the actual abundance of *S. elegans* (————) and *S. setosa* (– – – –) in half-hour oblique hauls with the 2-metre ring-trawl during the period March, 1935, to December, 1936.

Below, the percentage composition of the Sagitta populations during the same period; *S. elegans*, black; *S. setosa*, white; no Sagitta, cross-hatched.

At the top of the diagram the arrows indicate the mean direction (true) of the flow of water through the Straits of Dover for each month as indicated by the Carruthers Current Meter working from the Varne Lightship, kindly supplied by Dr. J. N. Carruthers. (Continued from Russell, 1936, p. 599, Fig. 2.) (*=*S. setosa*, 1; *S. elegans*, 2.)

of Muggiaea throughout the second half of the year possibly explains the preponderance of *S. elegans* and also its low numbers. Such water as has filled the western end of the English Channel has not come from the west, where the water is rich in *elegans*, but from the south-west and has carried away with it small quantities from the boundary of the *elegans* water proper. I am indebted to Dr. H. W. Harvey for the information that the western end of the English Channel filled with water of low salinity early in the year. This appears at first in conflict with the occurrence of oceanic plankton animals, but it must be realized that along the French coast whence this water probably comes the steep-to coast will allow the

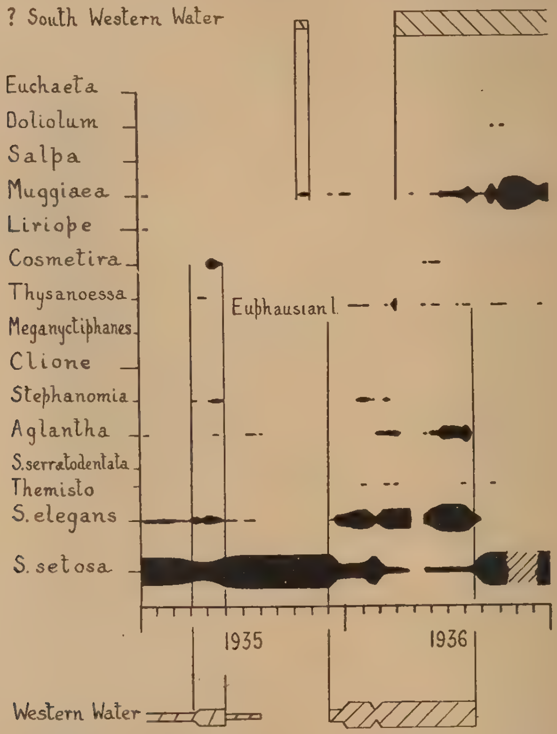

Fig. 3.—Diagram showing the occurrence of the various plankton indicators in collections off Plymouth during the years 1935 and 1936. (Continued from Russell, 1936, p. 599, Fig. 3.)

The Muggiaea species were *M. kochi* up to January, 1936, and thereafter in 1936 *M. atlantica*. The cross-hatching indicates a period during which no standard collections were made. *M. atlantica* was shown by tow-net collections to be numerous off Plymouth during that period. The Doliolum species was *D. nationalis*.

occurrence of oceanic plankton animals well inshore. It is possible that the improvement in the numbers of the young of summer spawning fish may bear some relation to these water movements.

From September until the end of the year *S. elegans* was almost completely replaced by *S. setosa*, while the presence of some south-western water was also indicated by the persistence of Muggiaea. An unusual record on December 31st, 1936, was that of the Scyphomedusan, *Discomedusa lobata* Claus, which has never before been recorded in these waters.

In Fig. 4 are shown the temperatures at L5 (surface) and E1 (bottom) in the early months of the year. Compared with other years 1936 was a late year, and the occurrence of such of the young of spring spawners as were taken was in agreement with this. It can, however, hardly have been the cause of the disappearance of the usual peak of young of spring spawners. Neither can their disappearance be accounted for by the depredations of ctenophores as was suggested for 1929 (1935, p. 166, Fig. 7). Ctenophores were very scarce in 1936 until September, when there was a sudden invasion, chiefly of Pleurobrachia, whose numbers were as follows :—September 15th, 3 ; 22nd, 2940 ; 29th, 14,020 ; October 6th, 1740 ; 12th, 3. Mr. P. G. Corbin has told me that Pleurobrachia were present in large numbers at E1 on September 18th, apparently already moving in towards the Eddystone.

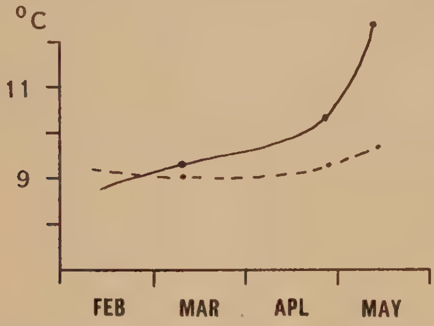

Fig. 4.—Temperatures in February, March, April and May for the year 1936. ——— surface at L5 ; – – – – bottom at E1.

We can thus at present only account for the failure of the production of the young of spring spawners as being due to the prolonged period of poverty in nutrient salts that has continued since 1932. In 1935 the spring peak was already considerably smaller than normal. If a renewed total annual abundance of young fish is to take place it must presumably await an influx into the English Channel of water rich in nutrient matter from the west in the winter months.

The year 1936 has been outstanding for the prolonged abundance of the eggs of the pilchard. These appeared first in numbers on March 31st and were last seen on October 12th, after which collections ceased until the middle of December. Their occurrences were as follows (approximate numbers, when counted, in brackets):—March 31st, many (2500): April 7th, few; 15th, few; 22nd, many (1750): May 4th, many (1430); 13th, very many; 20th, many: June 2nd, many (2000); 12th, many; 16th, very many (8000); 26th, many (3300): July 13th, very many (17,400); 24th, very many (5750); 29th, few: August 17th, present; 28th, present: September 1st, present; 9th, few; 15th, many (1500): October 6th, present; 12th, many (3160). The numbers of surviving young, however, do not appear to have been high.

It can now be stated that as in previous years the curve of the abundance of young whiting in the plankton still follows that for the landings of whiting (cf. 1935, p. 169, Fig. 8; 1936, p. 602). The landings of whiting by British sailing trawlers in area VII, d–e, in the English Channel fell in 1935 to 2·0 cwt. per 100 hours' fishing, and the sum of the average monthly catches of young whiting dropped to 13. This is excessively low when compared with 308 in 1932.

My thanks are due to Capt. V. Lord and the crew of the S.S. *Salpa* for their continued care in making these collections.

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TABLE I.

Dates on which Collections were made, 1936.

All 2 miles east of Eddystone unless otherwise stated.

(No observations between October 12th and December 16th.)

Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
1	5	12	7	4	2	13	5	1	6‡		16
7	12*	16	15	13	12	22†	11	9	12		21*
14	18*	23	22	20	16	24	17	15			31
21		31	28	27	26	29	28	22			
29								29			

* Haul taken at L4–L5.

† Haul taken 4 mi. S.S.E. of Mewstone.

‡ Haul taken 4 mi. E.×S. of Prawle Point.

TABLE II.

Average Monthly Catches of Post-larvae per Half-hour Oblique Haul with 2-metre Ring-trawl, 1936.

(No observations between October 12th and December 16th.)

	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total Young Fish	67	654	75	38	167	375	251	65	14	63		94	1863
Ditto, less Clupeids	21	27	30	31	104	111	112	29	14	6		2	487
All Clupeid spp.	46	627	45	7	63	264	139	36	+	58		92	1377
Clupea harengus	–	–	–	–	–	–	–	–	–	–		92*	92
Gadus pollachius	–	–	1	1	–	+	–	–	–	–		–	2
Gadus merlangus	–	–	3	1	7	2			–	–		–	13
Gadus minutus	–	+	1	1	1	4	–	–	–	–		–	7
Gadus luscus	12	1	2	–	–	+	+	–	–	1		+	16
Gadus callarius	–	–	–	–	–	–	–	–	–	–		–	–
Onos spp.	–	–	12	5	12	2	1	–	+			–	32
Molva molva	–	–	–	–	–	–	–	–	–	–		–	–
Merluccius merluccius	–	–	–	–	–	–	+	–	–	1		–	1
Raniceps raninus	–	–	–	–	–	–	1	–	–	–		–	1
Capros aper	–	–	–	–	–	–		–	–	–		–	–
Zeus faber	–	–	–	–	–	–	–	–	–	–		–	–
Arnoglossus sp.	–	–	–	–	–	3	2	2	1	–		–	8
Rhombus laevis	–	–	–	–	–	–	–	–	–	–		–	–
Rhombus maximus	–	–	–	–	–	–	+	–	–	–		–	+
Scophthalmus norvegicus	–	–	+	1	8	9	1	–	–	–		–	19
Zeugopterus punctatus	–	–	+	1	2	3	1	–	–	–		–	7
Zeugopterus unimaculatus	–	–	–	–	+	–	–	–	–	–		–	+
Pleuronectes limanda	–	+	+	2	12	4	–	–	–	–		–	18
Pleuronectes flesus	–	–	–	+	1	–	–	–	–	–		–	1
Pleuronectes microcephalus	–	–	–	–	1	2	–	–	–	–		–	3
Solea vulgaris	–	–	–	–	1	+	–	–	–	–		–	1
Solea variegata	–	–	–	1	6	12	3	–	–	–		–	22
Solea lascaris	–	–	–	–	–		–	–	+	–		–	+
Solea lutea	–	–	–	–	–	1	+	–	–	–		–	1
Serranus cabrilla	–	–	–	–	–	–	–	–	–	–		–	–
Caranx trachurus	–	–	–	–	–	–	+	1	8	1		–	10
Mullus surmuletus	–	–	–	–	–	–	–	–	–	–		–	–
Morone labrax	–	–	–	–	–	–	–	–	–	–		–	–
Ammodytes sp.	7	22	5	2	–	–	–	3	1	–		–	40
Ammodytes lanceolatus	–	–	1	4	2	4	4	2	–	1		–	18
Cepola rubescens	–	–	–	–	–	–	–	–	–	–		–	+
Callionymus spp.	–	–	3	12	50	52	49	2	1	1		–	170
Labrus bergylta	–	–	–	–	1	1	–	–	–	–		–	2
Labrus mixtus	–	–	–	–	+	1	+	–	–	–		–	1
Ctenolabrus rupestris	–	–	–	–	–	1	9	8	–	–		–	18
Crenilabrus melops	–	–	–	–	–	2	2	1	–	–		–	5
Centrolabrus exoletus	–	–	–	–	–	–	–	–	–	–		–	–
Trachinus vipera	–	–	–	–	–	–	–	1	–	–		–	1
Scomber scombrus	–	–	–	–	–	1	8	4	–	–		–	13
Gobiid spp.	2	1	–	–	1	4	10	1	–	1		1	21
Lebetus scorpioides	–	–	–	–	–	+	+	–	–	–		–	+
Blennius ocellaris	–	–	–	–		–	–	–	–	–		–	–
Blennius pholis	–	–	–	–	–	+	1	–	–	–		–	1
Blennius gattorugine	–	–	–	–	–	2	18	5	+	–		–	25
Chirolophis galerita	+	1	1	–	–	–	–	–	–	–		–	2
Agonus cataphractus	–	1	–	–	–	–	–	–	–	–		–	1
Trigla spp.	–	–	–	–	–	1	1	–	1	2		–	5
Cottus sp.†	–	+	2	1	–	–	–			–		–	3
Liparis montagui	–	–	–	–	–	–	–	–	–	–		–	–
Lepadogaster bimaculatus	–	–	–	–	–	1	+	–	–	–		–	1
Lophius piscatorius	–	–	+	–	–	+	1	–	–	–		–	1
Young Pipe-fish	–	–	–	–	–	1	–	–	1	–		–	2

* On Dec. 16th there was a catch of 274; this was immediately after a heavy gale and the contents of the catch were typical of a night haul. This average may therefore be unduly weighted.

† While I was in Copenhagen last year Dr. A. Fr. Bruun kindly drew my attention to a paper in which he described the young stages of what he presumed to be *Cottus lilljeborgi* (Public. Circ. No. 88, 1925). A re-examination of a number of specimens in my collections has shown that they agree with Bruun's figures for *C. lilljeborgi*, although the adult has not yet been recorded here. These post-larvae had previously been included under the name *C. bubalis*.

The Biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.).

By
C. M. Yonge, D.Sc.,
University of Bristol.

With 6 Figures in the Text.

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INTRODUCTION.

THE genus Aporrhais comprises a small number of species which are easily recognizable owing to the greatly expanded outer lip of the shell, and which occur in the North Atlantic from West Africa to the Arctic. The animals are of especial interest on account of their habits and also of their close relationship to the tropical family Strombidae, the two most important genera of which, Strombus and Pterocera, are characteristic members of coral reef faunas, the latter in the Indo-Pacific, the former in both this region and the Atlantic.

Two species of Aporrhais occur in the Norwegian fjords, *A. pes-pelecani*, which is also a member of the Plymouth fauna, and *A. serresiana* (=*A. macandreae*) which is an inhabitant of deeper water and is found only off the northern shores of Great Britain. This paper is the result of observations carried out on these two species at the Bergens Museum Biological Station at Herdla during the month of August, 1936. The author wishes to express his sincere thanks to the Director of the Station, Professor A. Brinkmann, for his great kindness and help and also to Amanuensis D. Rustad for much assistance. Acknowledgements are also due to the Colston Research Society of the University of Bristol for financial assistance.

APORRHAIS PES-PELECANI.

This species (Fig. 1) is characterized by a solid shell, the spire of which is longer than the expanded lip or " body." The latter is prolonged into four conspicuous digitations and a fifth which is only very slightly developed. The terminal or " caudal " digitation is notably stout and, owing to lateral dilation, blade-like (see Fig. 1). The point is directed downwards as shown in Fig. 2. This downward curve increases with age because, after the attainment of full size with the complete formation of the expanded lip, further shell formation is confined to an increase in thickness (very well-marked in the most worn shells), while, for reasons which will be made clear later, the frontal upper surface of the tip of the terminal digitation is worn away.

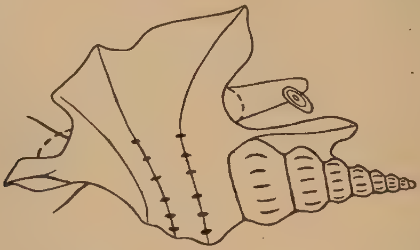

FIG. 1.—*Aporrhais pes-pelecani,* seen from above when moving over a hard surface. The head, except for the tentacles, is obscured by the blade-like terminal digitation. The operculum is attached to the upper side of the posterior end of the foot. The broken lines mark the positions, when the animal is buried, of the inhalent and exhalent apertures. × 1½.

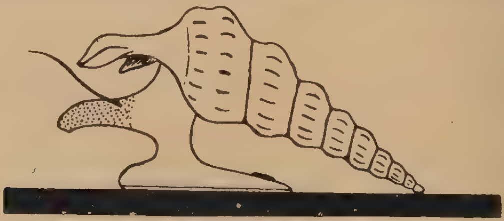

FIG. 2.—*A. pes-pelecani,* lateral view from left side showing the mode of progression over a hard surface.* The animal is raising the shell off the ground by extending the " neck," the body and shell will then be moved forward. × 1½.

The exposed regions of the animal are yellowish-white with red speckling which often extends over the foot, including the sole. The snout and head are thickly speckled with scarlet, while the tentacles are mingled yellow and scarlet. The foot (Figs. 1 and 2) is narrow and very extensile and carries the small, elongated operculum (Fig. 1) on the upper surface near the posterior end. It is united to the body by a thick "neck" or stalk (Fig. 2). The head is prolonged into the characteristic proboscis, the mouth opening at the end of this and consisting of a perpendicular slit. The tentacles (Figs. 1, 2 and 4) are long and slender when fully expanded and at the base of these, situated on prominent bulbs, are the eyes (Fig. 4).

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* Weber (Z. vergl. Physiol., II, 109 ; 1924) has described and figured this arhythmical movement in Chenopus (= Aporrhais) and also in Conus and Strombus.

(a) *Habitat and Habits.*

A. pes-pelecani is found on comparatively firm muddy gravel bottoms. In the neighbourhood of Herdla it was most abundant near Rossland on a bottom of this type at a depth of some 20 metres. It is characteristic of the shallower depths in which such bottoms occur; both Forbes and Hanley (1853) and Sars (1878) give the vertical distribution as from about 5 to 100 fathoms.

The animal is, in the words of Jeffreys (1867), "shy, slow and backward in its movements." When placed in a dish of sea-water the animals soon expand, locomotion taking place by a series of somewhat ungainly movements. The body is first raised by extending the "neck" (as shown in Fig. 2) which may stretch to a length of 1 cm., especially when faced with obstacles. Then, the foot remaining motionless, the body and the shell are carried forward in one convulsive movement for a distance up to about 8 mm. The shell and body then fall and the foot glides forward for the same distance, after which the "neck" is again raised and the process repeated. When placed upside down the animals can right themselves. This they do by extending the foot and head to the maximum extent around the base of the terminal digitation on the side away from the expanded lip. Extension proceeds until the foot is placed firmly on the substratum and, with the aid of the purchase so obtained, the shell is righted by a convulsive contraction of the body musculature.

It is interesting to compare these movements with those of the related "spider-shell" of the tropical Indo-Pacific, *Pterocera crocata*, which, although very much larger, has a shell of somewhat similar type. This animal lives on sandy areas on coral reefs. As previously observed (Yonge, 1932), it progresses by a series of sudden movements not unlike those of Aporrhais, but in this case not with the aid of a creeping sole, which has been lost, but by means of the stout operculum, long and very sharp, which is dug into the sand before each movement, after which it is dragged forward and pushed into the sand again.* In this case the animal can right itself by extending the foot around the same side of the shell as in Aporrhais until the operculum is hooked under the shell where this rests on the ground. Then, by a convulsive movement, the animal turns over.

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* Parker (J. Exp. Zool., XXXVI, 205; 1922) records similar progression in *Strombus gigas*.

When *A. pes-pelecani* was placed in a vessel containing a thick layer of gravelly mud it soon became apparent that the animal is actually specialized for burrowing and that progression on the surface must normally be of rare occurrence. After moving about for a short time on the surface the animals invariably began to burrow. The process is interesting. The terminal digitation, in shape admirably fitted for this, is first pushed beneath the substratum. Then, as a result of a succession of movements, the animal gradually progresses at first obliquely downward and then horizontally beneath the surface. The movements, which at first occur at intervals of between 40 seconds and one minute, become less frequent as the obstacles to progression increase. At each movement the animal turns over a little to the right side (that with the expanded lip) and the shell, as indicated by the movement of the mud above it, is raised. The action is clearly the same as when the animal is moving on the surface. As the animal sinks below the surface a small mound is raised in front of it and it is when this is some 5 mm. above the highest point on the terminal whorl of the shell that the direction of movement becomes horizontal. The upper surface of the apical whorls of the shell are still uncovered but lie in an elongated depression into which material falls from the sides and particularly from the mound raised in front. Finally, by a combination of the effect of continued forward movement and the falling in of material from all sides the shell is completely covered, as indicated in Fig. 3.

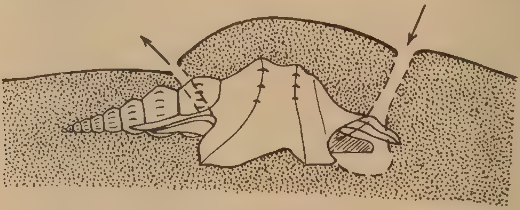

FIG. 3.—*A. pes-pelecani*, semi-diagrammatic representation of the position of the animal when buried, from the right side. The inhalent and exhalent apertures are indicated by arrows showing the direction of the currents. × 1½.

At this stage further movements can still be detected though with little or no progression. Each movement, by causing a raising and lowering of the expanded lip, results in the ejection of water from under the hinder margin of the expanded lip. In this way a temporary opening is formed in the gravel. There is no other opening at this stage. These movements probably serve to clear away the softer mud before the animal finally settles down ; they may also clear a space below the expanded, horizontally disposed lip.

Finally all movements cease. An inhalent opening is then made by the highly extensile proboscis which extends around the right-hand side of the terminal digitation, in front of the expanded lip, and upward until it breaks the surface. It then moves round actively in all directions curling back over the opening, so that the inhalent opening, at first irregular in outline, becomes finally rounded and some 2 mm. in diameter. Mucus is secreted by numerous unicellular glands in the wall of the proboscis (demonstrated in sections) and this consolidates the wall of the inhalent opening. The proboscis is then withdrawn, turned backward under the expanded lip and protruded upwards around the edge of the bay at the hinder end of the lip. An exhalent opening is formed in exactly the same manner as the inhalent one, the positions of both being shown in Fig. 3. The function of these becomes at once apparent when carmine is added to the water around them, a steady flow of water passing into the anterior one and out by way of the posterior one. The formation of two siphonal openings by the same agency, and at such considerable distance from one another—an animal of shell length 3·8 cm. had siphonal openings 2·3 cm. apart—has not, as far as can be ascertained, been observed in any other animal. It provides a most interesting example of adaptation in a burrowing Gastropod. The formation of siphonal tubes consolidated with mucus is also unusual in Mollusca although, during the same period at Herdla, it was found that the lamellibranch, *Thracia pubescens*, forms siphonal tubes in somewhat the same manner (Yonge, 1937).

After the inhalent and exhalent apertures have been made and consolidated the proboscis is withdrawn and only very occasionally protruded through them again, apparently to strengthen the lining of the tubes. It can always be induced to protrude by obliterating either of the openings which it promptly proceeds to reconstruct. The animals remain motionless beneath the surface, the only indication of their presence the two small openings, for long periods. One animal remained so for three days before uncovering itself, when it moved about for a short distance and then burrowed again. The proboscis can presumably range about at will under the surface of the expanded wing and both in front of and behind this, and it is to be assumed that the animal remains in one position so long as sufficient food can be obtained within this area.

(*b*) *Currents in the Mantle Cavity.*

The powerful inhalent and exhalent currents which enter and leave the apertures constructed by the proboscis reveal the presence of strong ciliary currents within the mantle cavity. It is also clear that, living buried beneath mud, the animals must be exposed to great danger from silt blocking the mantle cavity and must possess adequate mechanisms for dealing with this. The nature of the various ciliary mechanisms was revealed when the mantle cavity was opened, by cutting along the right side, as shown in Fig. 4.

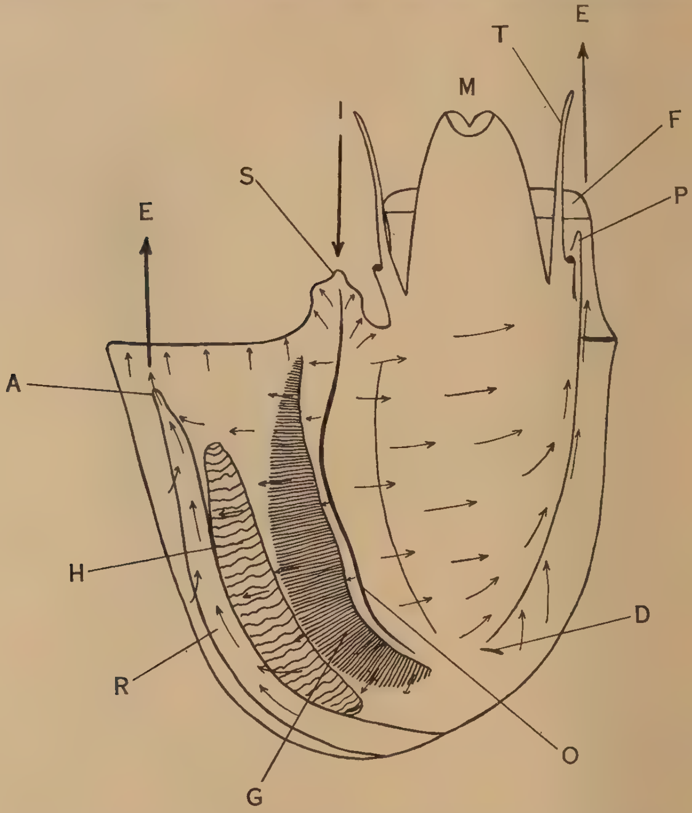

FIG. 4.—*A. pes-pelecani*, mantle cavity opened along the right side, seen from above. × 5. A, anus; D, opening of the male reproductive duct; E, exhalent current; F, anterior margin of foot; G, gill; H, hypobranchial gland; I, inhalent current; M, mouth; O, osphradium; P, penis; R, rectum; S, siphonal extension; T, tentacle with eye on bulb at base. Arrows indicate direction of ciliary currents.

The respiratory current is created by lateral cilia on the gill filaments, each of which consists of an elongate triangle, broadest at the base but slightly flattened at the tip. The large size of the gill (G) explains the powerful nature of this current. The inhalent current (I) enters on the left side of the head, where the mantle is extended to form a short siphonal process (S). The exhalent current (E) leaves the mantle cavity on the right side (topographically behind the other).

In the intact animal the siphonal process when distended is considerably larger than it appears in Fig. 4. It then extends for some distance forward under the terminal digitation and around the adjacent edge of the bay on the front edge of the expanded lip of the shell. The largest particles which are carried in with the inhalent current come in contact with the surface of the mantle in this region and are caught in powerful outwardly directed ciliary currents which also extend all around the edge of the mantle, as indicated by the arrows in Fig. 4.

The osphradium (O) is unusually elongated. It arises a short distance anterior to the extreme posterior end of the gill (G), running parallel to the base of this for some two-thirds of its course then diverging somewhat to the right and extending for some distance anterior to the gill along the middle line of the siphonal extension. The line of the osphradium marks the extreme left-hand side of the mantle cavity and therefore the middle line of this when it is cut open and extended as in Fig. 4. Under these conditions the ciliary currents on the mantle carry particles in opposite directions on either side of the osphradium. On the right-hand (ventral) side particles are carried over the floor of the mantle cavity to the exhalent region where they pass forward alongside the genital groove. On the dorsal side (left side in the figure) particles are carried to the gills, in between the filaments of which the water passes, where they are carried to the tip by the frontal cilia and thence, over the surface of the large hypobranchial gland (H) which secretes large quantities of mucus, to the region of the rectum (R) where they pass forward. The two mucus-laden streams of particles from the ventral and dorsal surfaces of the mantle cavity thus combine on the right or exhalent side of the mantle cavity and pass out, together with faeces discharged by the anus (A) at the side of the head. They are then carried downwards over the "neck" region into a groove running around the base of the foot in which all this waste material is conveyed backwards. All material which drops on to the foot is also carried into this tract.

The powerful respiratory currents, necessary possibly in view of the probably lowered oxygen tension in the water immediately in contact with mud containing much organic matter, are thus provided by the lateral ciliation on the filaments of the very well-developed gill. Disposal of material in suspension is brought about by three agencies. (1) Largest particles are immediately carried to the edge of the inhalent region, in essentially the same manner as similar material is ejected from the inhalent cavity of Lamellibranchia (see Kellogg, 1915; Yonge, 1923, 1926). (2) Somewhat lighter particles, which settle to the surface farther within the mantle cavity, are carried across the floor of the mantle cavity to the exhalent region. (3) The lightest particles of all, which are retained in suspension, are carried to the tip of the gills when the water passes through this and are then entangled in mucus secreted by the hypobranchial gland before passing out with the medium particles and the faeces by way of the exhalent opening.

(c) *Feeding.*

The animals will feed on the surface as readily as when buried and so the process can be observed. The proboscis continually moves about, being capable of extension from base of tentacles to tip up to a length of 1 cm., while the mouth continually searches the ground for food. The lateral lips are very sensitive and repeatedly open, exposing the small, but powerful, radula and the jaws (capable of firmly seizing a needle inserted into the mouth) which are protruded between them. Aporrhais has been described as a carnivore (Woodward, 1875), but is actually, as will be shown, a specialized herbivore. The presence of animal matter (shredded out tissues of bivalves) may even cause the animals to move away, sometimes backwards, or this may first be tasted and the proboscis then withdrawn sharply, the animal passing elsewhere. Finely cut up pieces of Fucus were not accepted, but fine green algae, such as shredded strips of Enteromorpha, were taken readily. This was seized by the jaws and radula and swallowed whole. The radula consists of a single hooked and denticulate tooth with three laterals, the first two transverse and the third claw-shaped (see Woodward, 1875, Fig. 100). A radula of this type has usually been considered characteristic of carnivorous Gastropoda (e.g. by Digby (1902) in Chytra and Limnotrochus), but is actually adapted for seizing, as opposed to scraping, which is the more usual method of feeding in herbivorous Gastropoda. The radula of Aporrhais, as Woodward has pointed out, most closely resembles those of Strombus and Pterocera (both herbivorous, Yonge, 1932) and of the Heteropod Carinaria, a carnivore which is specialized for seizing larger members of the zooplankton. This misapprehension as to the true significance of this type of radula is probably responsible for the statements that Aporrhais is a carnivore.

The animal presumably feeds normally by collecting, by means of the extensile proboscis, all particles of plant matter which occur in the mud in the region below and around the expanded lip. This material will consist largely of detritus of vegetable origin, the remains of algae or of diatoms which have dropped from the surface, together with bottom-living diatoms. Hunt (1925) in his work on the food of the bottom fauna around Plymouth classified *Aporrhais pes-pelecani*, together with one other Gastropod, *Turritella communis*, as a selective deposit-feeder. He did so as a result of examination of the stomach contents which he found always consisted of "roughly sorted bottom material."

(*d*) *The Alimentary Canal.*

Further evidence as to the nature of the food is provided by a study of the gut. A straight and comparatively wide oesophagus carries material into the large and complex stomach (Fig. 5). Into the lumen of this projects a stout crystalline style, 8 mm. long and 1 mm. wide in an adult animal. This structure, the presence of which was noted by Digby (1902), is secreted within a wide style-sac (S) in restricted communication with the first portion of the intestine (I). The head of the style bears, in life, against a similarly well-developed gastric shield (G). The presence of these organs immediately indicates that the animal is herbivorous, because, for reasons given elsewhere (Yonge, 1930), the presence of a crystalline style is incompatible with that of an extracellular protease, and, as already noted, the only possible substitute for this mechanical trituration by the radula, is absent. A second structure of great significance in the stomach is the series of parallel ridges which constitute

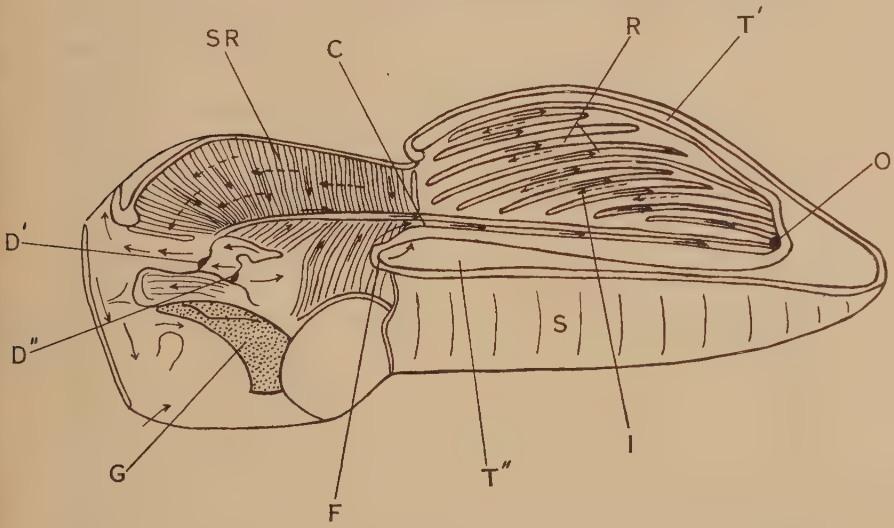

FIG. 5.—*A. pes-pelecani*, stomach with initial region of intestine and style-sac opened along mid-dorsal side. ×9. C, channel leading into initial region of intestine from sorting region in stomach; D′, D″, ducts into digestive diverticula; F, flap guarding entrance from oesophagus; G, gastric shield; I, initial region of intestine; O, opening into second region of intestine; R, ridges in initial region of intestine; S, style-sac; SR, sorting region; T′, T″, typhlosoles which separate style-sac from intestine. Arrows indicate direction of ciliary currents.

a sorting region (SR). Fine particles are carried over these ridges from summit to summit (as indicated by the broken arrows in Fig. 5) and so passed to the vicinity of the openings of the two ducts into the digestive diverticula (D′, D″), while larger particles pass into the grooves between the ridges and are conveyed by different ciliary tracts into a channel (C) which carries them rapidly into the first portion of the intestine.

The stomach of Aporrhais thus bears a remarkably close resemblance to that of a typical Lamellibranch in the presence of a style with an associated gastric shield and of a complicated sorting region (identical in function with those of Modiolus (Nelson, 1918), Mya (Yonge, 1923), Ostrea (Yonge, 1926) and Ensis (Graham, 1931)). It resembles the stomach of Pterocera and *Vermetus novae-hollandiae* (Yonge, 1932) in the presence of a style, but a sorting mechanism is absent or only very slightly developed in these animals. In Pterocera such an organ is probably of no importance, because the food, which is exclusively of plant origin, is exposed to the action of a powerful cellulase—absent (as experiments proved) in Aporrhais—which breaks down the larger food masses. In Vermetus the more finely divided nature of the food (collected by ciliary mechanisms) may render elaborate further sorting unnecessary.

The action of the stomach, therefore, is to convey fine particles into the ducts of the digestive diverticula and larger ones into the first portion of the intestine. There is an outward passage of particles along the floor of the ducts from the digestive diverticula (indicated by arrows in Fig. 5) and an inward movement above this. It is therefore possible for material to be carried in, and for the indigestible remnants of intracellular digestion to be later expelled. Muscular movements may also assist in this ; the walls of the stomach were observed to make frequent contractile movements even after being opened out, and this applied particularly to the flap which separates the two ducts and that which guards the entrance from the oesophagus (F). Within the stomach circulation of particles will be assisted by the rotation of the style, the dissolution of which will bring about extracellular digestion of starch. Sections of the digestive diverticula revealed the absence of secreting cells. The cells are presumably concerned exclusively with intracellular digestion as in other herbivorous Prosobranchia, such as Patella (Graham, 1932), and in all Lamellibranchia.

The intestinal regions of the gut are three in number and are concerned exclusively with consolidating the particles passed on from the stomach into firm faecal pellets. The regions consist of a wide initial region (I, Fig. 5) which is largely separated from the adjacent style-sac (S) by two typhlosoles (T′, T″), a narrow " small " intestine which ramifies for some distance through the viscera, and a terminal, much wider "rectum" (R, Fig. 4), which runs along the right side of the mantle cavity to open at the anus (A) in the exhalent region.

The channel (C) into which material is passed from the sorting region of the stomach is continued throughout the wide initial region of the intestine, which also possesses an interesting series of ridges (R) which run obliquely around it as shown in Fig. 5. On the summits of these powerful ciliary currents carry material into the opening into the "small" intestine (O) towards which the ridges converge. In the grooves between the ridges less powerful currents beat in the opposite direction. There is a great production of mucus in this region of the intestine and the purpose of the ridges and grooves with their different tracts of cilia is apparently that of thoroughly mixing the particles with mucus. Muscular movements play an important part in this process, continual contractions, causing the temporary obliteration of the grooves, being frequently observed even after this region had been opened out. The material passed into the opening of the "small" intestine is thoroughly mixed into a homogeneous mass with large quantities of mucus.

The "small" intestine has a narrow lumen with no typhlosole, but with a fine groove on one side which probably represents the continuation of the channel in the stomach and initial region of the intestine. A powerful anally-directed ciliary current is present in this groove. The faeces are here consolidated into a firm, continuous thread with an outer envelope of mucus. In this form they enter the wide "rectum." The groove with its powerful ciliary current is continued and provides the propulsive force towards the anus. The remainder of the wall of the rectum is ciliated, but the direction of the currents could not be determined with accuracy. When carborundum was placed upon this surface it merely trembled to and fro. The same action is always observed when similar particles are placed on the surface of the style-sac epithelium of any Lamellibranch (or style-bearing Gastropod), indicating that in the rectum also the cilia may only act when material is pressed tightly against them (Yonge, 1926). Additional evidence is provided by a similar velvety appearance of the surface of the living epithelium in both rectum and style-sac and by a general resemblance of both epithelia in section. It is certainly true that both epithelia have the same function, that of moulding material into a rod-like form. In the rectum of Aporrhais the fine threads which enter from the "small" intestine are converted into elongated, thick pellets, each of which contains a twisted coiled mass of these finer threads enclosed in a second, thicker envelope secreted by the walls of the rectum. Thus it is in the form of large pellets, which cannot foul the water in the mantle cavity, that the faeces are expelled from the anus.

Aporrhais serresiana.

This species provides an interesting contrast in structure and habitat to *A. pes-pelecani*. The shell, illustrated in Fig. 6, attains a slightly greater size than that of *A. pes-pelecani*, but is somewhat more delicate, notably in the expanded lip. Owing to the greater length of the terminal digitation in this species (compare Figs. 1 and 6) the spire is shorter than the " body " of the shell. The expanded lip is much larger than in the other species and there are five, instead of four, prominent digitations, which are prolonged into fine points instead of ending bluntly. The terminal digitation is notably long and narrow, being straight and pointed instead of broad and blade-like as it is in *A. pes-pelecani*. The animal is more delicate than that of the other species and the tissues are white and translucent except for the head and proboscis. The former possesses a triangular patch of red on the dorsal surface, while the latter is speckled with scarlet along the dorsal surface, with a white line, widening near the tip, running along the middle line. The tentacles are translucent with an opaque white band running along the upper side. They are also longer and more extensile than those of *A. pes-pelecani*, being capable, in a fully grown animal, of extending to a length of 1·5 cm.

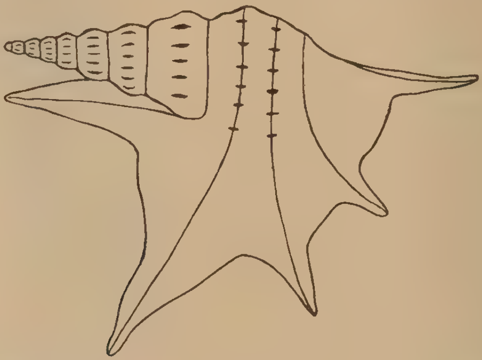

Fig. 6.—*A. serresiana*, shell seen from above, the great extent of the expanded lip is shown, also the five sharply pointed digitations, the terminal one being notably fine. × 1½.

A. serresiana is an inhabitant of deeper water than *A. pes-pelecani*. Sars (1878) states that the vertical distribution is from 80–300 fathoms. It was collected in greatest numbers, although it is never so abundant as *A. pes-pelecani*, at depths of about 200 metres in the Herdla fjord, where it was the only species of the genus taken. At intermediate depths, notably about 60 metres at Ypsøsund, both species were taken in proportions of roughly seven *A. pes-pelecani* to one *A. serresiana.* Neither species was as abundant as they are in shallower or greater depths respectively.

The distribution of the two species is clearly dependent on the nature of the bottom. *A. pes-pelecani*, as already stated, occurs on comparatively firm bottoms of muddy gravel, but *A. serresiana* is an inhabitant of softer bottoms of fine mud found in deeper water.

The habits of *A. serresiana* are the same as those of *A. pes-pelecani.* It moves in the same manner over the bottom of a glass dish and burrows into soft mud. When placed on muddy gravel taken from the normal habitat of *A. pes-pelecani*, one specimen burrowed into the side of a small mound and moved slowly horizontally under the surface. No attempt was made to push downwards nor was there the same "shouldering" action as in the other species. Only with much greater effort and over a much longer period did the animal finally bury itself. *A. serresiana* is definitely less powerful than *A. pes-pelecani* and possibly in its natural habitat tends to sink in the mud and then push forward rather than actively to burrow downwards. The shape of the shell can be related to the needs of the animal. The elongated, pointed terminal digitation is well adapted for pushing through soft but closely compacted mud, while the greater extent of the expanded lip and the lighter shell prevent it from sinking too far below the surface.

When *A. pes-pelecani* was placed on soft mud it moved about less easily than the other species, tending to flounder in it and being hampered by great accumulations of mud in the mantle cavity and on the foot. The animal made no attempt to burrow in the mud, but rather tended to raise the body as far as possible clear of the bottom. The animal was most clearly not adapted for life on such a bottom.

Examination of the genital organs of *A. serresiana* failed to reveal the presence of a brood-pouch for incubating the young, so it is probable that pelagic larvae are produced similar to those of *A. pes-pelecani* described by Lebour (1933). If this is so then the survival of the young of the two species, after they descend at metamorphosis from the surface waters, must depend on the type of bottom on which they fall (itself usually dependent on the depth). Young *A. pes-pelecani* which settle down in deep water will be unable to exist on the soft mud, and young *A. serresiana* will be similarly unable to burrow, and so find adequate protection, on stiff muddy gravel bottoms at moderate depths. In certain intermediate regions both species will be able to exist, though conditions will be ideal for neither and the population of both will be correspondingly sparse.

Both in the form and solidity of the shell and in the strength of the body the two species are clearly adapted for a similar mode of life on different types of bottom and the fact that these occur at different depths explains the differences in the horizontal distribution. The reduced pigmentation of the body in *A. serresiana* is presumably the result of the reduced light in the greater depths where it lives.

DISCUSSION.

The genus Aporrhais consists of Gastropods adapted for burrowing in mud and collecting beneath the surface of this detritus of plant origin by means of an extensile proboscis. The manner in which they maintain contact with the water above represents a further adaptation of the proboscis and one which, so far as our present knowledge extends, appears to be unique amongst the Gastropoda. The mode of life resembles more that of a Lamellibranch than of a Gastropod, the majority of mud-living species of which are carnivorous, such as Buccinum, Murex or Nassa, which plough their way through the mud in the search for prey. It is, however, possible that Turritella, which as shown by Hunt (1925) has similar stomach contents, and just possibly Cerithium and Caecum, may prove to live in a somewhat similar manner to Aporrhais. The interesting freshwater genera, Chyta and Limnotrochus, from Lake Tanganyika have similar feeding and digestive organs (Digby, 1902), but nothing is known of their habits. They are certainly related to Aporrhais and to the Strombidae.

The characteristic expanded lip of the shell in the fully grown animal is not necessarily primitively an adaptation concerned with the burrowing habit. In the first place young specimens of *A. pes-pelecani* in which the terminal whorl has not yet been formed, and also older specimens in which the terminal whorl is present but the expanded lip has still to be formed, were both found capable of burrowing like the adults. These will also burrow, although with certain difficulty, when the terminal digitation has been broken off. In the second place a similar expanded lip occurs in the allied Strombidae—very well developed in Pterocera, less so in Strombus, but absent in Rosellaria—none of which live in the same manner. In Pterocera (Yonge, 1932) this flattening of the shell enables the animal to move about on the surface of the sand *without* sinking into this and to keep the right side up despite the ungainly, jerking movements referred to earlier in this paper. Strombus possesses somewhat similar habits ; those of Rosellaria are unknown to the author. It appears not impossible that the expanded lip of Aporrhais may originally have been evolved in connexion with a similar mode of life, but that the animals later took to life on mud instead of sand and then to burrowing in this with consequent changes in the form of the terminal digitation and in the breadth and flatness of the lip. There can be little doubt that both are of importance to the adult animals, the terminal digitations in the manner described for the two species, and the horizontal shelf provided by the lip in the increased area over which the proboscis may browse unimpeded and, in *A. serresiana*, possibly by the increased resistance to sinking in the softer mud.

The powerful water currents through the mantle cavity due to the great development of the gill, and the elaboration of the ciliary mechanisms for disposing of sediment carried in with the respiratory current (the latter better developed in *A. serresiana*) are both of them adaptations to the mode of life. They have an added interest because they indicate the manner in which ciliary feeding in Gastropods such as Crepidula (Orton, 1912) and *Vermetus novae-hollandiae* (Yonge, 1932) may have evolved. The mechanism for rejection of large particles from the inhalent opening may have become modified to form the food pouch in Crepidula, and the rejection currents in the exhalent region to form the food channel. The further flattening of the tips of the gill filaments and the appearance of cilia carrying particles forwards in this region would convert the gill into the food-collecting organ of Crepidula, or *Vermetus novae-hollandiae*. It is hoped to develop this argument in more detail elsewhere.

The mode of feeding is very similar to that of Pterocera, the radula and jaws having a similar selective action and the teeth of the radula being few in number to permit of seizing instead of rasping. The form of the gut is that of an herbivorous Gastropod, most notably in the presence of a well-developed crystalline style and gastric shield which, as shown elsewhere, occur in herbivorous Gastropoda which " feed by ciliary mechanisms, or by the slow but almost continuous action of a radula " (Yonge, 1932). It is certain that, if it is to obtain adequate supplies of vegetable detritus having food value, Aporrhais must constantly be feeding. The differences between Aporrhais and Pterocera consist in the presence of a powerful cellulase in the latter—necessary because fresh algae, not decomposing detritus, are swallowed intact and there is no means of mechanical trituration—and the presence of an elaborate sorting mechanism in the stomach of the former—the result of the varied size of the particles collected by the proboscis and the necessity of ensuring that only the smallest of these shall pass into the ducts of the digestive diverticula for intracellular digestion. The remainder of the gut in Aporrhais is concerned exclusively with the elaboration of faeces, of profound importance, as Graham (1932) has emphasized in Patella, in Gastropoda (and other Mollusca, Yonge, 1935) in which the anus opens into the mantle cavity, fouling of which must be rigidly prevented.

NOTE ADDED IN PROOF. Since this paper appeared in proof, Mr. R. Winckworth, in the course of a most helpful letter on the nomenclature of the northern species of Aporrhais, has pointed out that Kobelt (1906,

p. 17) considered *A. serresianus*, described by Sars (1878, p. 198, pl. xii, fig. 7), to be merely a deep-water form of *A. pes-pelecani* and so re-named it *A. pes-pelecani sarsii*. The significant differences recorded in this paper between the form of the shell, the form and pigmentation of the exposed portions of the body, and the reactions to different types of bottom, in *A. pes-pelecani* and *A. serresiana* lend little support to this view. Moreover, the fact that both were taken in the same haul of the dredge at intermediate depths, appears convincing evidence that *A. serresiana* is a true species.

SUMMARY.

1. *Aporrhais pes-pelecani* occurs on muddy gravel at moderate depths and is specialized for burrowing in this.

2. The mode of burrowing is described and also the formation of mucus-lined inhalent and exhalent openings by the proboscis.

3. There is a powerful respiratory current through the mantle cavity which also possesses three sets of ciliary currents for disposing of sediment carried in with this.

4. The animal is a specialized detritus feeder selecting only material of plant origin. The radula consists of one central and three lateral teeth on each side, an indication that it is used for seizing as opposed to scraping, *not* that the animal is carnivorous.

5. The stomach possesses a well-developed ciliary sorting mechanism. The large crystalline style and gastric shield indicate that the animal is herbivorous, but there is no cellulase.

6. The intestine is divided into three regions which are concerned exclusively with the gradual elaboration of the large elongated faecal pellets.

7. *A. serresiana* occurs in deeper water on a soft mud bottom. The differences in the form of the shell and the strength of the body between this species and *A. pes-pelecani* can all be correlated with the difference in habitat of the two species.

8. The form and the mode of life of both species are compared with those of the allied Strombidae of tropical coral reefs, and the ciliary mechanisms in the mantle cavity with those of ciliary feeding Gastropoda.

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Larval and Post-larval Lima from Plymouth.

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With 4 Figures in the Text.

Two species of Lima are known from Plymouth : *Lima hians* (Gmelin), the commonest species, inhabiting small patches of stones with muddy gravel at extreme low-tide mark on the north side of the Breakwater, where many individuals may be found together, and *Lima loscombi* Sowerby, found on the coarse grounds west of the Eddystone, Rame–Eddystone Grounds, Mewstone Grounds, Stoke Point Grounds and south-west of the Eddystone (see Marine Biological Association, Plymouth Marine Fauna, 1931). The latter is a much smaller species than the former, not so highly coloured, and much rarer. Although it is often difficult to obtain *Lima hians*, as it is only accessible at very low tides, it occurs in numbers in the locality cited.

Whilst investigating the lamellibranch veligers in the plankton one was found which stood out from the rest on account of its triangular wedge-shaped shell, most of the lamellibranchs being round or oval in their free-swimming stages. In 1914 Odhner, describing some veligers from Rovigno in the Adriatic, showed that *Lima inflata* Lamarck has a similarly shaped shell and his figures and descriptions agree in essentials, both in animal and shell, with those from Plymouth. Miyazaki (1935) reared the larvae of *Lima brasilanica* Adams and Reeve from artificial fertilizations up to the late veliger stages in Japan, but his latest veligers were much rounder than either *Lima inflata* or the Lima from Plymouth.

The Plymouth veligers were picked out from the fresh plankton and placed in plunger-jars with some food consisting of small flagellates and diatoms. The water in the plunger-jars was from outside the Breakwater and was not sterilized nor filtered : it must thus have contained minute plant food. The veligers grew well and soon lost the velum, reaching a stage when they were easily recognizable as Lima. As they are much commoner in the inside plankton than in the outside, it seems almost certain that they belong to *Lima hians*, although it has not been possible to rear them farther than to a shell breadth* of 2 mm., at which stage

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* The breadth of the shell is measured from the umbo to the ventral margin, the length from the anterior to the posterior margin.

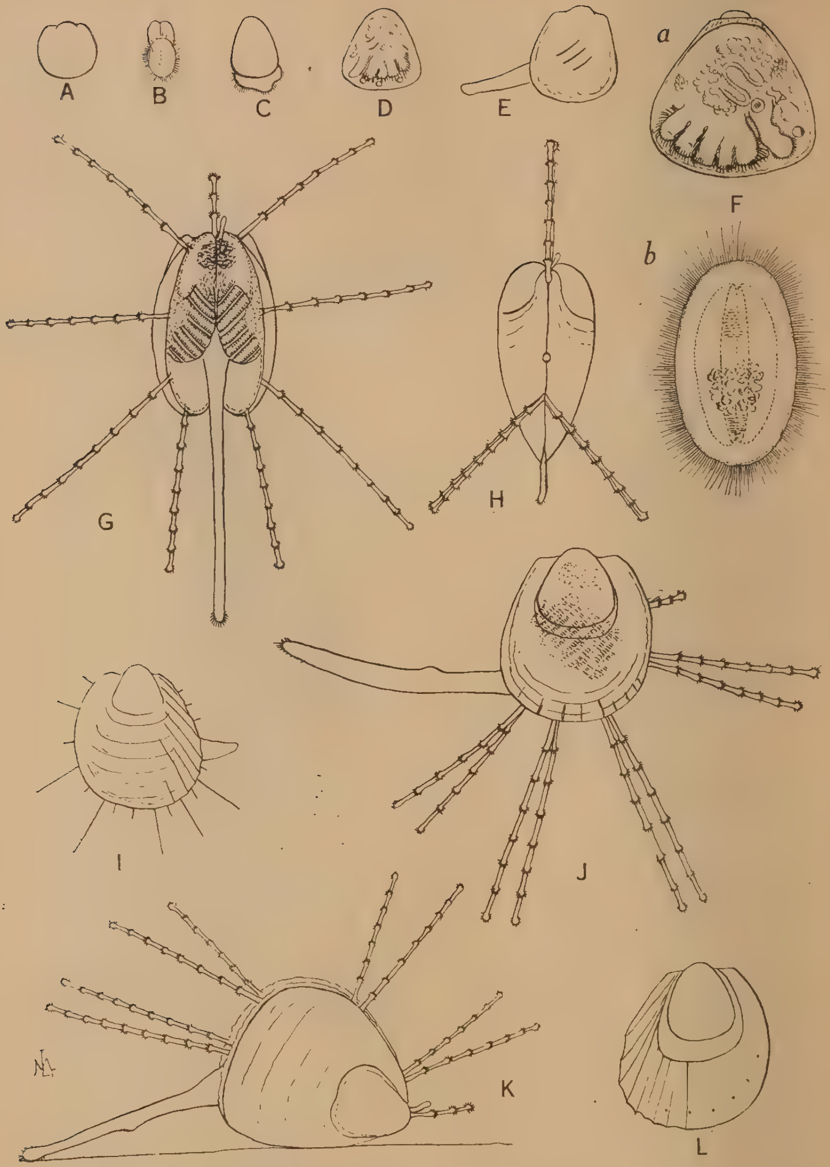

Fig. 1.—Lima larvae and post-larvae.

A. Smallest larva from plankton, 0·08 mm.
B. Veliger, 0·16 mm.
C. Veliger, 0·24 mm.
D. Veliger, 0·30 mm. showing rudiments of tentacles.
E. Latest veliger, 0·32 mm. (*a*, lateral view, velum withdrawn; *b*, swimming, from above).
F. Post-larva, having lost velum, 0·35 mm. across.
G, H, J, K. Post-larva grown in plunger-jar from veliger, shell 0·64 mm. breadth. (G, from above, valves open; H, from above, valves closed; J, side view; K, side view crawling).
I. Young Lima, 1 mm. across, grown in plunger-jar.
L. Young Lima, 1·28 mm. across, grown in plunger-jar, showing eyes through the shell.

the animal was still almost colourless and the shape and markings not distinctive of either species.*

These Lima veligers occurred in the plankton from August to April. They were completely absent in the early summer and reached their maximum abundance about October, when it was possible to pick out 70 to 90 specimens from one tow-net haul. They occurred most plentifully in the tow-nettings from inside the Breakwater or just outside it, although often present in small numbers in the outside waters as far as Station L4 (half-way to the Eddystone) or slightly beyond this.

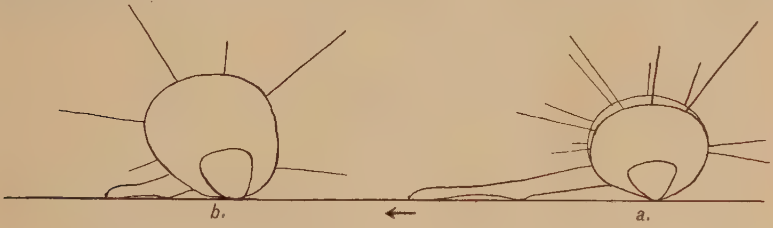

Fig. 2.—Post-larval Lima crawling. (*a*) Valves open. (*b*) Valves closed.

Besides the unusual shape of the larval shell it is the very peculiar method of progression in the young bottom stages that makes Lima so specially interesting. The adult animal is provided with a mass of long and contractile ciliated tentacles. In the very young bottom stages only a few of these tentacles are developed and they are used to help the animal as it crawls. This, however, is not done by their action on the ground surface, for they are stretched out freely into the water; it seems rather that they are used to balance the body as described below.

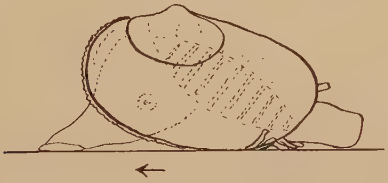

Fig. 3.—Post-larval Ensis, showing the usual method of crawling in lamellibranchs.

The smallest veliger seen in the plankton is almost round and is about 0·08 mm. in length and breadth (Fig. 1, A), having a straight hinge with toxodont teeth. This corresponds well with Odhner's youngest larva (1914). Later larvae (Fig. 1, B–D) have a broader shell, gradually becoming wedge-shaped with the widest part ventral. They sometimes vary in breadth in relation to the length, but usually the greatest length is about equal to the breadth. Just before metamorphosis the shell measures about 0·32 mm. in breadth (Fig. 1, E). At this size it loses the velum and goes down to the bottom. Three or four roundish prominences are to be seen just inside the mantle edge which are the beginning of the tentacles. The velum is large and overlaps the ventral shell margin. The foot, as is well known in the adult, has the peculiarity of being twisted in the opposite direction from all other known lamellibranchs, and this shows even in the early bottom stages, as has been noted by Odhner (*op. cit.*).

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* Since this was written, Mr. R. Winckworth has examined these reared post-larval shells and pronounces them to be, almost certainly, *Lima hians*.

When the velum is lost the shell grows, especially in breadth, the tentacles lengthen, increase in number and become ringed and ciliated. The animal takes up its position on the bottom with its hinge and anterior margin downwards, the posterior and ventral margin upwards. The foot, which is long and flexible, emerges antero-ventrally; the tentacles are extended and the valves open, showing the gills and mantle-margin (Fig. 1, G). The mantle-margin is thin and filmy, being enlarged ventrally as a soft veil-like outgrowth. The tentacles arise from just inside the margin. The ciliated foot is extended to its greatest extent and attached to the bottom: the tentacles also extend outwards and the valves are far apart. The muscles of the foot contract; the valves close; the pairs of tentacles, still extended, come together, and a sudden movement takes place in a leech-like manner, the animal being brought up to the fixed position of the foot (Fig. 2). This very extraordinary method of progression is unknown in any other genus. Odhner (*op. cit.*) described the movement of the very young bottom stages of *Lima inflata*: the foot directed backwards, the young shell creeping backwards, with the mouth posterior to the foot; but in the young Lima from Plymouth the tilt of the shell goes much farther and the hinge is almost on the bottom. Thus the direction of movement is antero-ventral and not actually backwards, although the mouth is behind the foot and the foot is twisted in the opposite direction to that of the ordinary lamellibranch young which crawls with the dorsal margin uppermost and the foot moving forwards (Fig. 3). This position with the hinge and anterior margin downwards and ventral and posterior margin upwards is the natural resting position of the adult Lima and also its position when it crawls. A figure (Fig. 4) is given here showing a small *Lima loscombi* in a bowl which always took up its position with its valves open, gills exposed and tentacles more or less outstretched. Jeffreys (1863, Vol. II, p. 89) quotes Canon Norman's description of *Lima hians* which when tired of swimming lies on its back, the valves expanded. In the recent paper by Studnitz (1931) there are good figures and descriptions of the normal position of the adult *Lima hians* and of the twisted foot in relation

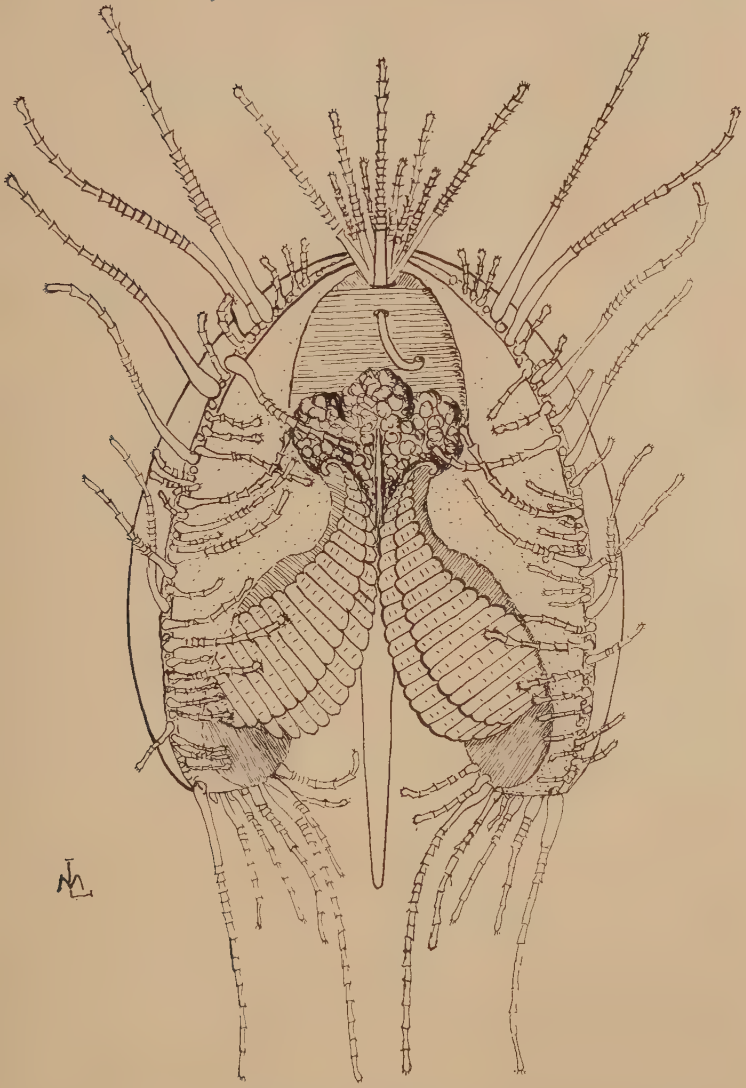

FIG. 4.—*Lima loscombi*, from Eddystone Amphioxus grounds, 8 mm. broad, in natural position on bottom.

to the other organs. He also describes, to a certain extent, the creeping movement with the position of the shell, but in the adult the enormous mass of tentacles must necessarily affect the movement and cannot be used in the same way as is described for the very young stages from Plymouth.

As the young shell grows, more tentacles are added between the others, some being longer with many rings (Fig. 1, G–K). In specimens reared in a plunger-jar there were 17 pairs of tentacles in one shell 1·5 mm. in breadth, and at 2 mm. there were 25 pairs. In the adult *Lima hians* there are hundreds, *L. loscombi* having much fewer.

The smallest veliger seen in the plankton must be very young and probably not much larger than the first shelled stage. Unfortunately it was not possible to collect adults with eggs and fertilization could not therefore be attempted.

All the free-swimming stages have shells glass-like in transparency with colourless animals, a faint pink tinge appearing in the young stages 2 mm. in breadth. The velum is bordered by very powerful cilia. Gills begin to appear in the latest veliger stage. The stomach is usually full of green or brown food and the digestive gland is of a conspicuous brown colour. There is a large otocyst at the base of the foot containing several otoliths. In specimens from 1 mm. in shell breadth there are well-formed red eyes round the inside of the mantle margin, looking very like those in similar stages of Pecten or Chlamys (Fig. 1, L).

Up to 2 mm. in breadth growth was quick, for veligers of 0·16 mm. grew to 0·32 mm. in a few weeks, and in two months they reached 1·5 mm. In two and a half months some were 2 mm. in breadth, but they never grew after this although some lived for months at this stage. Some of these were removed to glass dishes with sand and put under circulation, but they did not grow and made no nests. The oldest specimens at present alive are about four months old.

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A Comparison of the Biology of *Echinus esculentus* in different Habitats. Part III.

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With 3 Figures in the Text.

General.

In an earlier paper (Moore, 1934), an account was given of the season of spawning and the seasonal changes in the gonad volume of urchins from various depths in the Isle of Man. In order to compare these with urchins from a more southerly locality, monthly samples were taken in 1934–5 from 2 miles N. to N.N.E. of the Eddystone, in 27–28 fathoms, and in 1935–6 from $2\frac{1}{2}$–3 miles S. to S.S.W. of Revelstoke Point in 17–22 fathoms. The samples consisted of about fifty urchins each time, and the gonads of these were examined by smears in the usual way, their condition being recorded as the percentage of each sex which were respectively unripe, ripe, spawning or spent. The gonad volumes were expressed as the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$ (Moore, 1934, p. 871). These results, together with temperature observations kindly supplied by Dr. H. W. Harvey, are shown in Fig. 1. Unfortunately no temperature observations are available for the actual grounds on which the samples were taken, but they may be assumed to be very similar to those at station L4 which is half-way between Rame Head and the Eddystone. At this station temperatures were available up to August 1935 only, so the observations for station E1, 10 miles SW. of the Eddystone, are also included. Although at this deeper station the temperature range at the bottom is less extreme than at L4, yet at the critical period of spawning there is little difference. An eleven years' mean temperature curve for E1 is also included from which it will be seen that the summer of 1934 was distinctly cold and the following winter rather warm, while the summer of 1935 was normal, and the following winter rather cold. Whether there is any connexion between these temperature differences and the observed differences in the gonads in the different years is doubtful.

SEASONAL GONAD CHANGES AT PLYMOUTH.

As has already been stated, the degree of ripeness of the males is less easily defined with accuracy than that of the females. Considering the latter, therefore, it will be seen that practically no ripe females were found before the beginning of February in either year, and few before the beginning of March. Spawning commenced about the end of March in 1935 and the end of February in 1936, the time corresponding approximately with the time of lowest sea temperature. The date on which 50% of the urchins were spent, taking both sexes together, was May 3rd in 1935 and April 25th in 1936, corresponding to sea temperatures of about 9·7 and 9·2° C. The temperatures at a corresponding period in spawning in the Isle of Man were 7·0° C. in 1931 and 7·8° C. in 1932. Spawning takes place, therefore, at a higher temperature at Plymouth than in the more northerly locality, and falls at about the middle of the range of 4–16° C. given by Runnström (1927) for the normal development of *Echinus esculentus* larvæ.

The growth of the gonads at Port Erin was found to be very different on the two grounds "Breakwater" and "Breast." On the latter, at a depth of 17–20 fathoms, the gonads never filled up to a value of more than 0·4 for the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$. The gonads gradually regained size after spawning until they were at a maximum size about August, after which they remained constant until the winter and then shrank considerably, only regaining their full volume immediately before spawning. This winter shrinkage of the gonads was definitely not a second spawning, and seems more likely to have been associated with lack of food at that time. On the "Breakwater" ground, where the urchins live about low-water mark, the gonads filled up to a much greater size, with a ratio of nearly 2·0 compared with 0·4 on the Breast ground, and with no winter drop in volume. It seems probable that the greater abundance of food is here the controlling factor.

The Plymouth material appears to be of the Breast type, as might be expected from the depth from which it was taken. The gonad volume ratio was at a value of between 0·4 and 0·5 in the summer of 1934, but dropped somewhat in the winter, rising again only immediately before spawning in 1935. At their maximum the females attained a value of 0·7, being considerably bigger than the males of a corresponding test size, a phenomenon which was observed on both grounds at Port Erin also. After spawning in 1935 the gonads filled up slightly, but never reached nearly so great a size as they did the previous year, and the spawning in 1936 was extremely poor, the drop in volume of the female gonads being from 0·7 to 0·2 in 1935 and only from 0·3 to 0·2 in 1936.

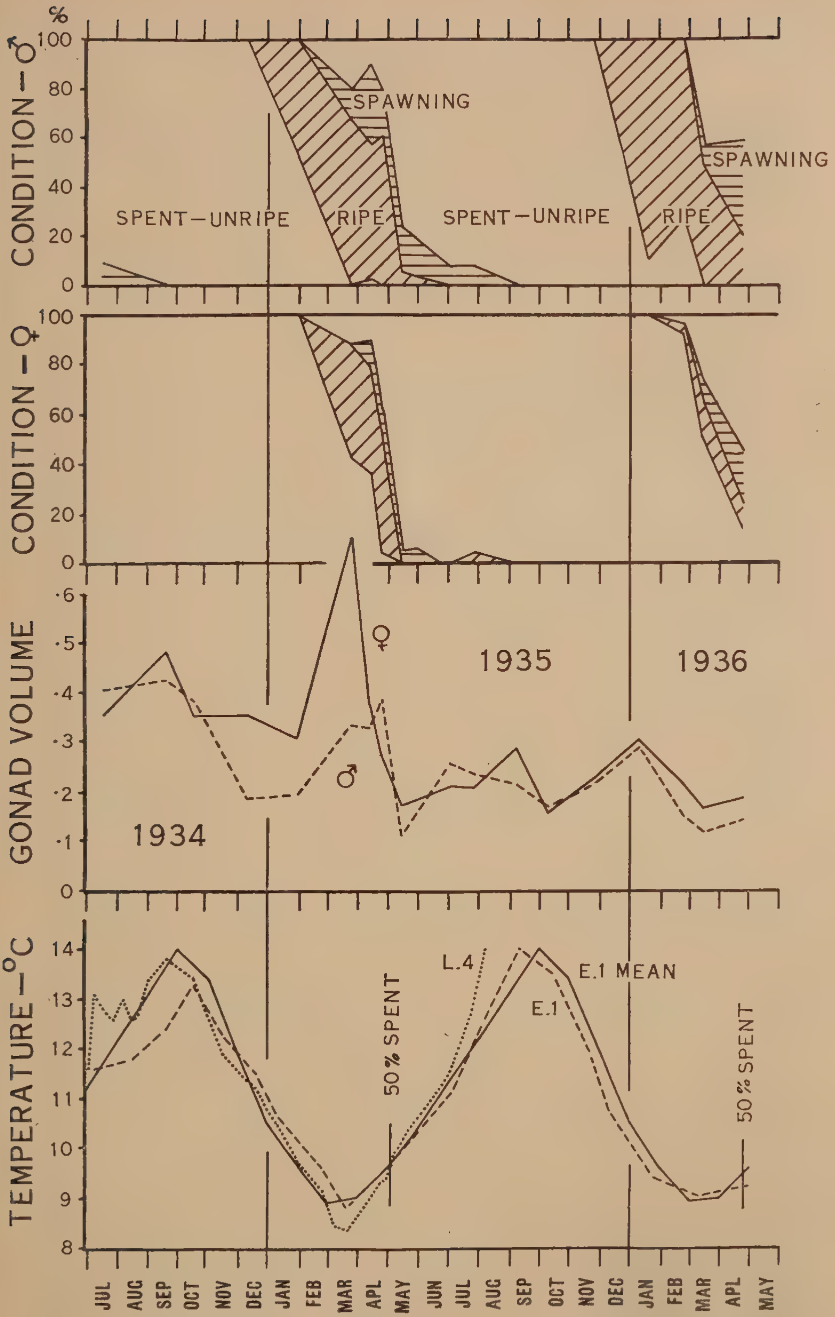

Fig. 1.—Seasonal changes in the conditions of male and female urchins from Plymouth and of their gonad volumes as indicated by the ratio $\frac{10 \times \text{Gonad volume}}{\text{Test volume}}$. Temperatures at the bottom at Stations L4 and E1 during the period under observation, and an eleven years' mean temperature curve for E1.

The difference between the two seasons may be due to the shift in the grounds from which the urchins were taken, but the two grounds are very similar in character and it seems likely that the differences were, in part at any rate, due to 1936 having been an abnormal year.

There appears to be a definite increase in the size of urchins southwards, as indicated in Fig. 2. It should be noted that in this figure the samples from Port Erin (Breast) and Plymouth are deficient in the smaller sizes, the curves having been abstracted from the records of gonad examinations for which the smaller sizes were rejected. Those for Port Erin (Breakwater) and for Millport are, however, complete. At Millport and Port Erin, specimens were never recorded over 121 mm. in breadth, corresponding

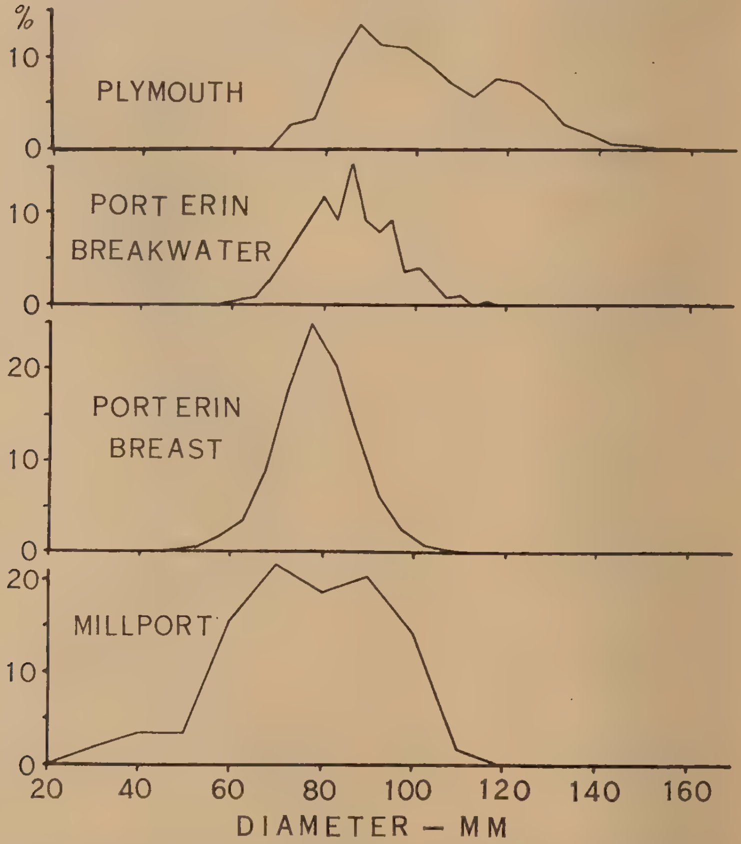

FIG. 2.—Mean size distribution curves for all samples examined from Plymouth, Port Erin (Breakwater and Breast) and Millport, showing greater size of urchins in the south (see text below).

to a volume of about 800 c.c. (external), whereas urchins were frequently taken at Plymouth with a diameter of 150 mm., corresponding to a volume of about 1800 c.c., and still larger specimens have been recorded.

Deposition of Pigment.

In colour also the Plymouth urchins resemble most closely the Breast urchins, the violet colouration of the test which was so frequent on the Breakwater, but rare on the Breast, having never been noted at Plymouth. Violet colouration of the spines is, however, frequently seen. The violet pigment is probably derived from some food, possibly algal, which is obtained more readily in the alga-covered littoral and sub-littoral zone than in deeper water. Griffiths (1900) has described a violet pigment with lipochrome properties from the integument of *Echinus esculentus*, while MacMunn (1885, 1889) has given the name Echinochrome to a reddish pigment occurring in the elaeocytes in the perivisceral fluid of *Strongylocentrotus lividus*, *Echinocardium cordatum* and *Echinus esculentus*. Later workers have studied a similar pigment found in the test, and McLendon (1912) and Cannan (1927) have described the same or a similar pigment from Arbacia at Woods Hole.

Dr. K. G. Stern (personal communication) when working on *Echinus esculentus* at Plymouth, found that this red pigment, which he calls Echinorubin, and which was similar to, although apparently not identical with that of McLendon and Cannan, was present in the elaeocytes of the body fluid and also in the test, but was present in far the greatest quantities in the walls of the intestine. The pigment appears to be absorbed into the intestine with the food, transferred to the elaeocytes in the body fluid, and finally excreted into the outer surface of the shell where it is deposited. I am indebted to Dr. Stern for permission to publish these notes on the amounts of pigment found by him in the intestines. The extraction with solvents of a large number of the latter, sent to him at intervals throughout the year, proved that the red pigment which was so abundant in the intestines in the summer and autumn, was absent from them in the winter and spring, its place being apparently taken by a brown oily substance. Table I shows the yields of echinorubin obtained by him from the intestines of the Plymouth urchins, but it must be realized that these are only notes on the yields obtained in the preparation of the crystalline substance, and not in any way quantitative analyses.

The tests of urchins from both grounds at Port Erin and also those from Millport showed the deposition of the red pigment, and of the violet one when present, in the period between about April and December (Moore, 1935). As, however, shell growth was confined to the period between November to January and the end of March, there being no further growth during the summer months, and since pigment laid down in the surface of the plates will remain at the surface until overlayed by a layer of non-pigmented shell at the next period of shell growth, there can be no evidence of the precise time at which the pigment is deposited beyond the fact that this occurs between the limits of about April and December. Since the pigment is now shown to be the same as that which is present in large quantities in the intestine during summer and autumn, it seems probable that the annual summer rings of pigment in the test represent periods of feeding on some particular diet, or quite possibly the main periods in which the urchin is feeding at all. On the other hand, the females from the Breakwater at Port Erin continued to show gonad growth right up to the time of commencement of spawning, and on all grounds where there is a drop in gonad volume in winter there is a corresponding rise just before spawning, presumably correlated with an increased supply of food at that time. It is noteworthy, however, that on the Breakwater ground, where algal food is abundant throughout the entire year, and where there is no winter drop in gonad volume, the pigment rings were sufficiently clear to be counted in only 46% of the urchins as compared with 79% on the Chickens ground farther offshore. And with regard to the source of the pigment, Awerinzew (1911) has shown a close correlation between algal and urchin pigments in the case of *Strongylocentrotus draebachiensis*. This species varies in colour from yellowish green to deep reddish purple, and it was found that urchins of the former colour occurred almost invariably on a substratum of sandy gravel while the reddish purple ones were found on the red calcareous alga Lithothamnion. Finally the reddish purple urchins soon began to lose their colour when taken into the aquarium. So it is very probable that here also the urchin is obtaining its pigment from the food that it eats.

TABLE I.

Date.	No. of urchins.	Yield of crude echinorubin crystals.	Notes.
1934.			
Sept.–	ca. 50	ca. 80 mg.	together yielding 50 mg. of recrystallized echinorubin.
Oct. 20	ca. 50	ca. 40 mg.	
Dec. 14	45	30 mg.	
1935.			
Jan. 11	ca. 50	35 mg.	
Feb. 2	ca. 50	trace only	extract yielded a brown oily substance.
April 18	?	trace only	
May 15	65	some	
May 23	18	none	

Deutler (1926) has demonstrated the presence of similar pigment bands in the plates of the urchin *Colobocentrotus atratus*. From these bands, he states, the age can be determined; and he shows that they are seen clearly in those echinoderms which feed at any rate to some extent on algæ, and which migrate into the littoral zone. He quotes a number of such urchins which live in the littoral zone, and some of which migrate in and out of it annually, and he suggests that the zonation of the pigment in their plates is due to a seasonal feeding rhythm which makes them deposit pigment in the summer at the time when they are feeding most.

If a large seasonal migration into and out of the algal region of the shore took place in *Echinus esculentus* this would necessitate such changes of diet as might well produce the observed seasonal differences in pigment, and some such migration has been suggested both at Millport (Elmhirst, 1922) and at Port Erin (Stott, 1931). The former, however, states that the migration is only from the actual intertidal zone down to a depth of one to two fathoms (where algæ are still very abundant), and so far as Port Erin is concerned I have never been able to satisfy myself that such a migration occurs at all. Certainly there is no such migration of the deep-water Chickens urchins which live at a depth of 35 fathoms and yet show clearly distinguished pigment zones. It must, therefore, be assumed that some seasonal rhythm of feeding occurs in both the littoral and the deeper-water urchins, and that the main difference between the two lies firstly in the greater food supply available in the littoral zone, resulting in larger gonads and absence of a winter drop in gonad volume, and secondly in a difference in the nature of the food as reflected in the greater frequency of occurrence of the violet pigment in the tests of the littoral urchins.

Outline of Seasonal Changes.

Reid (1935) has recently brought together what is known of the relation of *E. esculentus* to its external environment, and in Fig. 3 an attempt is made to summarize the existing knowledge of its internal changes, e.g. growth, spawning, etc., and the seasons at which they occur. Since the information available is incomplete, and of necessity drawn from different localities, the results must be taken as a generalization only, from which any individual locality may diverge considerably.

At the beginning of the year the shell starts to grow, and continues to do so up to some time between April and June, the exact time varying with locality and year. At the same time, on the offshore grounds, feeding appears to have slowed down, and the gonad which is the main reserve of food material has been shrinking since October–November. It is replenished, however, in February and March, and about March, when the sea temperature is at its minimum, spawning commences with concurrent shrinking of the gonad. Spawning continues until about May, by which time the gonad is beginning to fill up again, and this it continues to do until about August. In the case of the females only from the Breakwater, gonad growth continued right up to the commencement of spawning the following year. Stott (1931) has shown that in the period between December and the end of March, the percentage of glycogen in the gonad is dropping, possibly being transformed into some other form of carbohydrate. The time of pigment deposition in the shell is not clearly defined but almost certainly follows closely the time when there is abundant pigment in the walls of the intestine, that is from about May to January, and this probably corresponds with the main feeding period. In August–September the sea temperature is at its maximum, and it is about this time that shrinkage of the gonads of the offshore urchins commences.

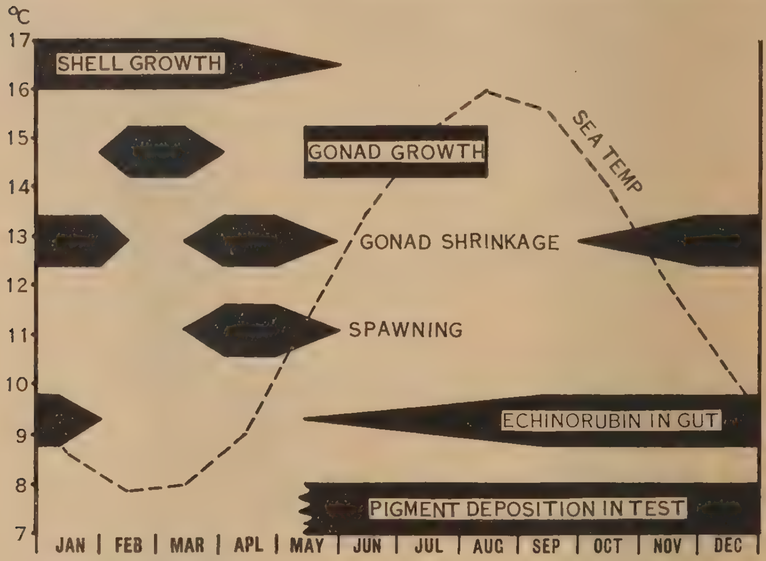

Fig. 3.—Generalized diagram of the seasons of shell growth, gonad growth, etc., in *Echinus esculentus*, with a sea temperature curve (for Plymouth).

SUMMARY.

1. Gonad examinations were made on monthly samples of *Echinus esculentus* from Plymouth in 1934, 1935, and 1936.

2. Spawning is from February–March to May, 50% spawning occurring at a temperature of 9·2–9·7° C. compared with 7·0–7·8° C. in the Isle of Man. There was a winter drop in gonad volume one year, but not the other.

3. The nature, distribution and source of the pigments in the shell are discussed, and it is shown that pigment is found in quantity in the intestine only in the summer and autumn.

4. The known facts with regard to the seasons of growth, spawning, etc., are brought together into a generalized diagram.

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The Biology of *Littorina littorea.* Part I. Growth of the Shell and Tissues, Spawning, Length of Life and Mortality.

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With Plate III and 10 Figures in the Text.

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MATERIAL AND METHODS.

THE Periwinkle, *Littorina littorea* (L.), is one of the most abundant gastropods on the shore, and can live under widely varying conditions. It is found on clean, alga-covered rocks, among small stones, on gravel, on soft mud, and rarely even on sand. It ranges from about high water of neap tides to extreme low water of spring tides, and in some places even slightly below this, although in most localities it is restricted to a much smaller part of the tidal zone. It occurs also from shores with high wave-exposure to sheltered and even polluted estuaries, where it is tolerant of considerable lowering of the salinity. The material for the present study was collected at intervals throughout 1934-1936 from three localities near Plymouth, the details of which are as follows.

Trevol. Level: mid-tide level. A mud flat in the middle of St. John's Lake, opposite Trevol Pier. The mud is soft, so that a man will sink six to twelve inches into it, and there is a sprinkling of dead shells on the surface. The smaller winkles in particular tend to cluster on these dead shells. In some parts there is a growth of Zostera and Enteromorpha, but on most of the ground there is no macroscopic algal growth.

Drake's Island. Winkles are abundant from about mid-tide level to between mean low water of neap tides and mean low water of spring tides. The area used for collection was a stony beach on the north side of the island, with a medium amount of Fucoid growth.

Misery Point, Yealm. The winkles are abundant about mean low water of spring tides, and very few are found above mean low water of neap tides. There is very little Fucoid growth, but the winkles cluster in very large numbers on such few fronds of Fucus as are present. There is a tidal stream of about 2½ knots past the point.

Single samples were also taken from four other localities for shape determinations (see p. 732).

A certain number of winkles are collected by fishermen from the Trevol and Yealm grounds, but mostly from slightly different positions from those used in the present work, so that the populations may be taken as being little influenced by them. There is no such collection on Drake's Island.

Two methods of sampling were used. The first, that of hand picking all the winkles visible on a fairly large area, yielded large numbers, but was not fully representative of the smaller sizes below about one centimetre in height. The second method consisted in sieving the entire surface sample of ground from a known area, down to about five centimetres in depth, but owing to the large amount of extraneous material collected this method could be applied to small areas only—in practice usually one square metre. The second method yielded a representative sample of all sizes of the population, with as many of the small sizes as were needed for measurement but did not contain anything like the one to two thousand of the larger sizes which were required. Where possible, therefore, the two methods were used and the size distribution of the larger sizes as determined from the large hand-picked sample combined with that for the smaller sizes as determined from the surface sample in the proportion indicated in the latter. This procedure was readily applicable on the mud at Trevol, where it was used from July, 1935, onwards. It was more difficult on the stony ground at Drake's Island and the Yealm, where it was applied on special occasions only; in general, only hand-picked samples were taken from these two grounds with the result that, while the mean height of the first year shells as determined from these samples is correct, their numbers relative to the older ones are too small. The same applies to the sample taken at Trevol before July, 1935.

The height of the smaller shells was measured to the nearest millimetre with sliding callipers. For the larger shells it was found necessary, if a second year peak was to be differentiated with any certainty in the size distribution curves, to measure between one and two thousand shells in each sample. For this purpose a machine was used which measured the height of each shell, and besides indicating its height in millimetres, counted the total number measured in each millimetre group. The average numbers measured per sample for each ground were 1,348 for the Yealm, 1,601 for Trevol and 706 for Drake's Island, the numbers being kept smaller at the latter locality owing to the limited size of the ground and the fear of seriously depleting its stock.

Samples were taken from each ground at approximately monthly intervals, and were used for size distribution analyses and also for shell and tissue weight determinations and for gonad examinations. At first twenty animals were taken at each millimetre interval of height and, after being boiled for about two minutes, the animals were removed from their shells with a pin, the twenty shells and twenty bodies being placed in weighed glass dishes. They were then dried in a boiling-water oven, the shells for one day and the tissues for three, and weighed. Monthly curves were thus obtained for each locality showing the relation of shell and tissue weights to shell height. After twelve months it was shown conclusively that there was no seasonal variation in shell weight, so the latter determinations were discontinued, and the mean values for the year assumed to hold for all further calculations (Fig. 6). In this part of the work the two sexes were not distinguished, but from July, 1935, onwards the material from Trevol was examined on extraction from the shells, and twenty each of males and females were set aside from each millimetre group for weighing. It was found to be quite possible to distinguish the sexes by the presence or absence of a penis, except in very small immature specimens, although in the non-breeding period the penis is reduced to a very small size.

From December, 1935, regular samples were examined from Trevol, and a few also from the other grounds, for the condition of the gonads. Smears were taken from the ovary and oviduct of the females and from the vesicula seminalis of the males, and the condition of the genital products recorded. In most cases samples were taken representative of each distinguishable year group on the ground in question.

Finally, for the determination of the growth of shells which were too old to come within the limit of distinguishable year-groups in the size distribution analyses, a number of winkles were collected from Drake's Island, marked at the apex with cellulose paint, and their lip notched with a carborundum wheel. They were then released on the ground from which they were taken and at intervals they were collected and the height and the spiral increment to the lip from the notch measured for each individual. They were then returned to the shore again as quickly as possible, care being taken to avoid high temperatures during the period when they were away from the shore ; it was usually found possible to collect them one day and to return them the next. The process of marking was calculated to produce as little disturbance as possible. The shells were rapidly dried in a current of air from an electric fan ; the apex of each was then dipped into cellulose paint and they were replaced in the air current until the paint was dry enough to handle. The edge of the shell was then notched with an electrically driven carborundum stone, and the winkles returned to running sea-water, the whole process not lasting more than half an hour. Cellulose paint was found to last fairly well on the shore and not to need renewing for several months at least.

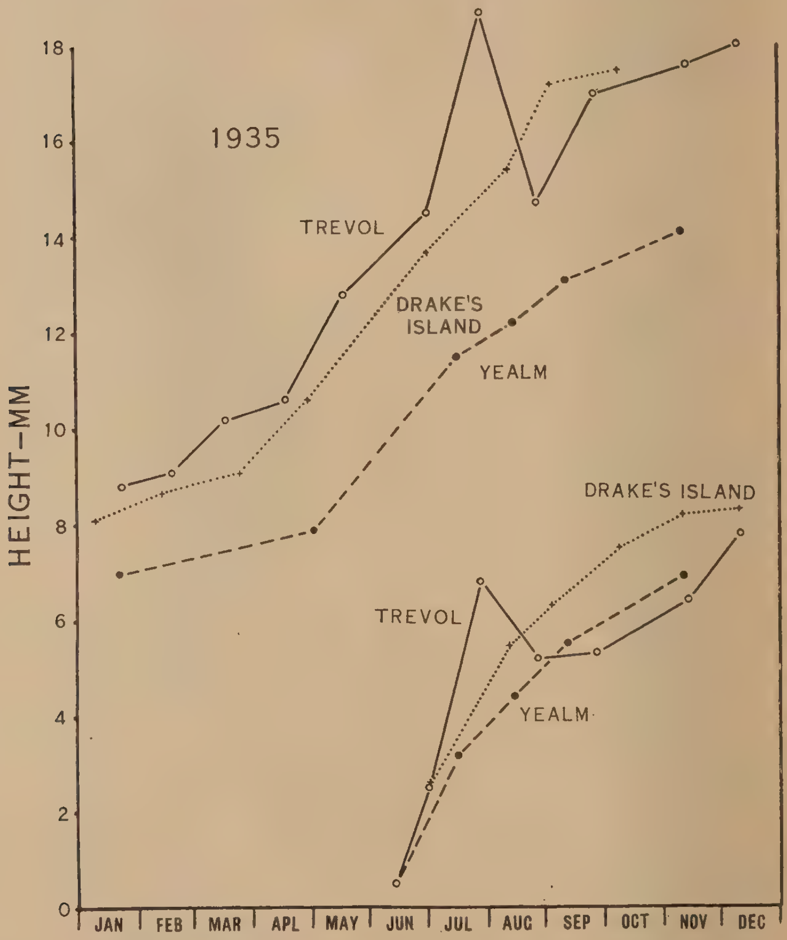

Fig. 1.—Growth of *L. littorea* on the three grounds in 1935.

In the first place 2,695 marked winkles were released on Drake's Island in September, 1934, and the returns obtained ranged from three to four hundred in the first few months down to about a hundred at the end of a year. Of these winkles, 1,700 whose sex was not determined, were marked with blue paint. The sex of the remainder was determined by relaxing them in a dilute solution of pilocarpine hydrochloride and noting the presence or absence of a penis. The males were then painted green and the females red. The measurements of the red and the green shells were kept separate for the determination of the relative growth-rates of the two sexes, but all colours were taken together for the general growth results.

Shell Growth.

The size distribution curves for the three grounds are shown in Plate III. It should be noted that the proportion of first-year shells to older ones is too low up to a height of about one centimetre on all grounds except for the 1935 brood at Trevol. From these size distribution figures the mean size of the first and second year groups was determined wherever possible for each sample, and from these the growth curves shown in Figs. 1, 2 and 3 were drawn. Fig. 1 shows the relative growth in height on the three grounds in 1935. In their first year, growth on Drake's Island was considerably faster than that at the Yealm, while the growth at Trevol was rather erratic. For the second year animals, however, the rates for Trevol and Drake's Island are very similar while that for the Yealm is definitely less. The figures serve also to show the variation in growth on the same

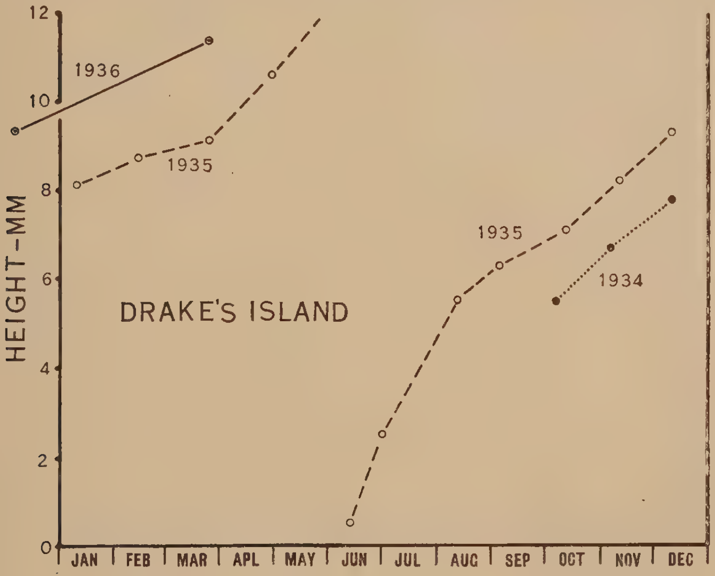

Fig. 2.—Comparison of the growth of *L. littorea* on Drake's Island in different years.

ground in different years (Figs. 2 and 3). At the Yealm there is no significant difference in the growth-rates in the years 1934, '35 and '36, but at Drake's Island the rate is definitely greater in 1936 than in 1935 and in 1935 than in 1934. At Trevol the reverse results are found, and the rate is less in 1936 than in 1935 and less again in 1935 than in 1934. The differences in successive years at Drake's Island and Trevol are of an order which might well be considered significant in correlation with, for example, sea temperature changes in the different years, and yet the winkles on the

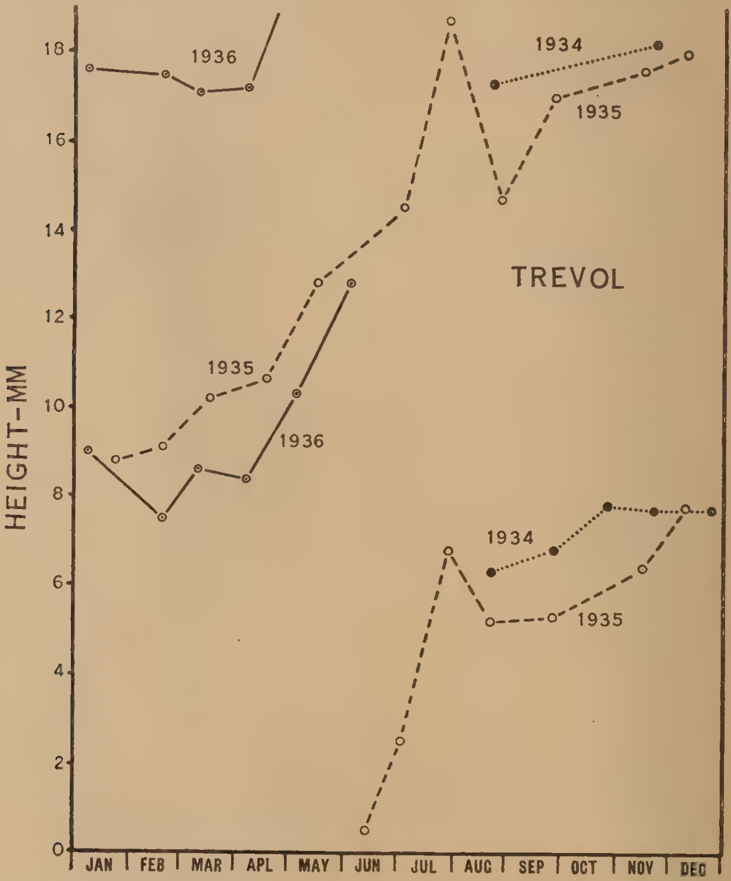

Fig. 3.—Comparison of the growth of *L. littorea* at Trevol in different years.

EXPLANATION OF PLATE III.

Size distribution curves for *L. littorea* for the three grounds.

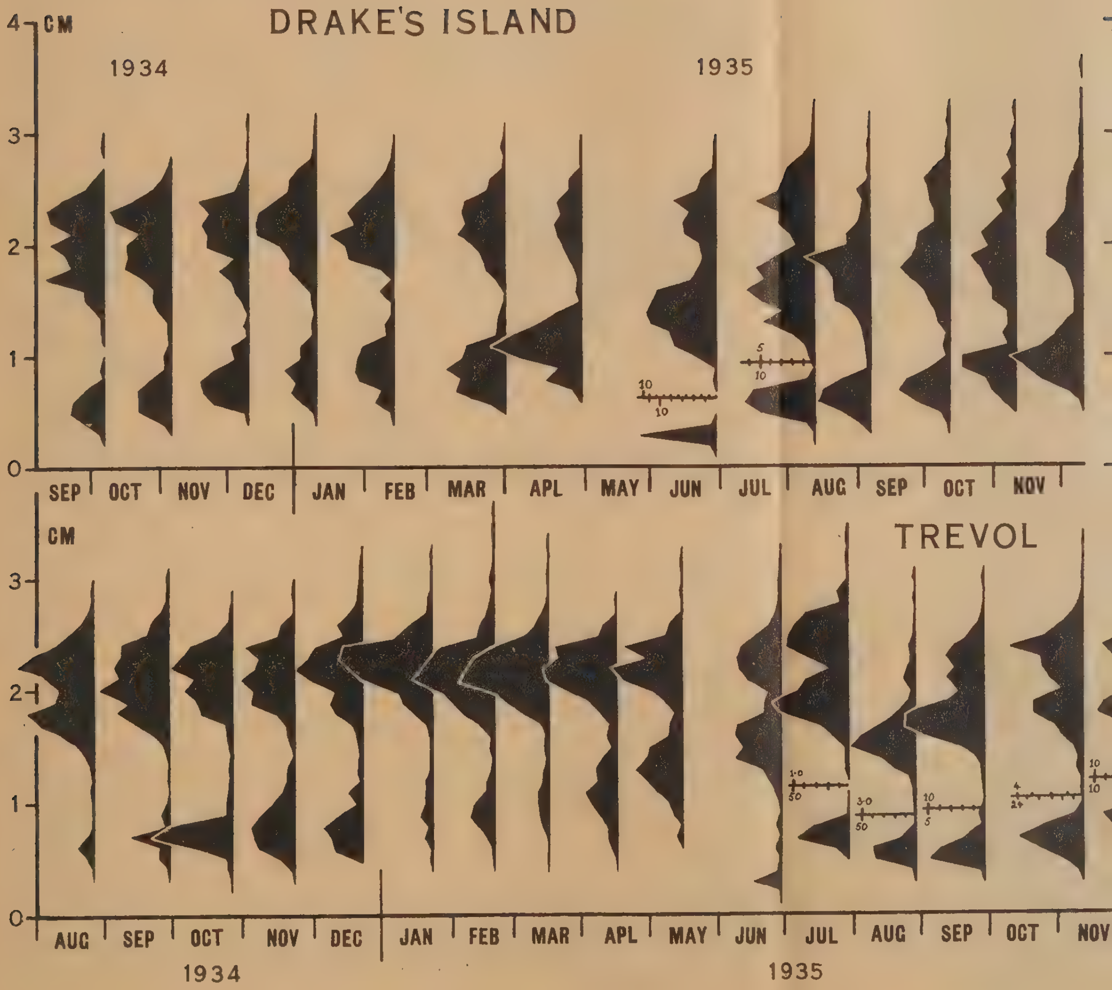
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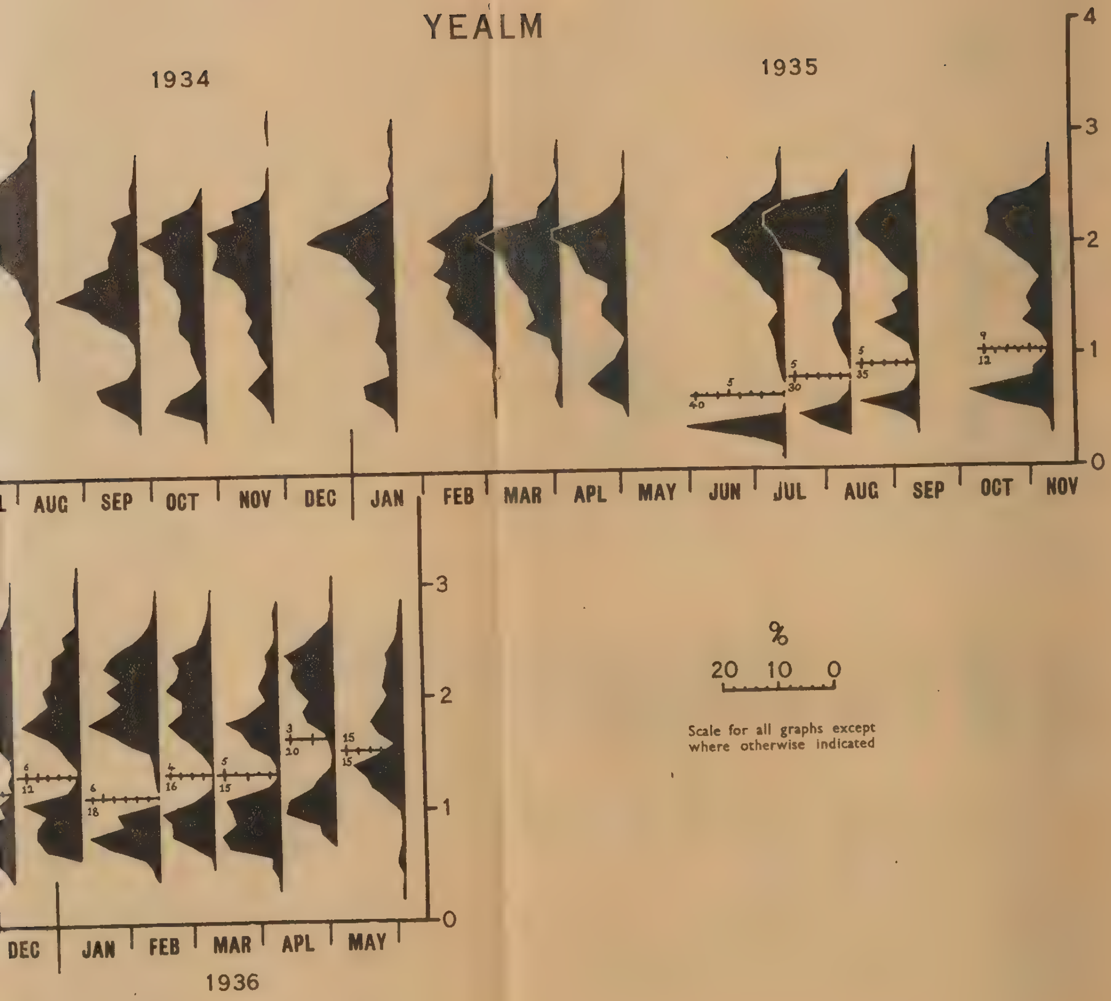
PLATE III



Scale for all graphs except where otherwise indicated different grounds show entirely different variations, thus emphasizing the danger of drawing conclusions from the study of a population from a single locality or for a single year only. The possible connexion between the observed local differences and the habitat is discussed later.

The size distribution figures are useful only up to an age of about two years, after which the successive peaks overlap too much to be distinguished, so for the growth of the larger sizes a method of individual marking was necessary. Such a method is possible only on a ground which is close to the laboratory, and where collecting is easy and there is no risk of the brightly coloured shells being picked up by fishermen, and for all these Drake's Island was ideal. A small number of marked shells were released at the Yealm also, but the returns were poor, and the results served only to confirm the much slower growth-rate there than at Drake's Island.

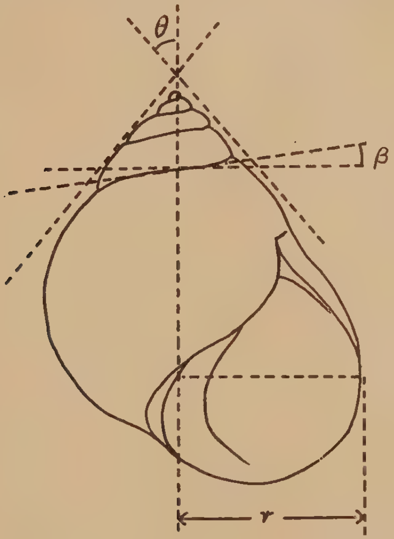


FIG. 4.—Diagram of *L. littorea* showing shell angles (see text).

The relation between the amount of growth measured in a spiral direction on the lip of a shell and the corresponding increase in the height of the shell is dependent on two fundamental shell angles, θ the half-apical angle (Fig. 4), and α the spiral angle (Moore, 1936, p. 72). θ is easily obtained by direct measurement, but α is more readily obtained from the formula

$$\tan \alpha = \frac{2{\cdot}72 \sin \theta}{\log R}$$

where R = the ratio of the diameters of two successive whorls. The formula for the length of a plane logarithmic spiral is $\frac{l}{r} = \sec \alpha$, where l=the length, and r=the vector radius (Fig. 4). In the case of a spiral projected on to a cone such as we have in Littorina, a correction must be made, so that

$$\frac{l'}{r} = \sec \alpha . \sec \beta$$

where l′=the spirally measured length, and β an angle derived from α and θ, but most readily obtained by direct measurement (Fig. 4). If the shell is supported over a mirror, and the angle between a suture and its reflection is measured with a protractor, this is equal to 2β. The radius and height are measured directly, and so a curve can be constructed relating lip increment to corresponding height increment at any given height of shell. (This is necessary since both α and θ vary with shell height.)

The successive readings for Drake's Island growth material were in the form of heights and lip increments, and these, shown as height increments plotted against initial height of shell at the time of marking, are shown in Fig. 5. The points on the extreme left of the curve were obtained from the growth in the first year as given by the size distribution analyses. The results are less consistent than could be desired towards the end of the experiment when the returns were dropping off in number, but they are sufficient to show that *L. littorea* is about 14 mm. high in December of its first year, 17·4 mm. in its second winter, 22·4 mm. in its third winter, 25·4 mm. in its fourth, 27·3 mm. in its fifth, etc. At this rate the very large individuals up to 36 mm. in height found in this locality would, if their growth-rate has been normal, be many years old, but there is always the possibility of their having grown at an abnormally high rate, perhaps as a result of parasitization by cercariae. It may, however, be mentioned that Waters (1890) says that he kept individuals living for ten years in an aquarium.

In the above calculations the possibility of a different growth-rate in the males and the females has not been considered, since it would obviously have been impossible to determine the sex of the sixty thousand shells measured. The experiment on the growth of winkles of known sex on Drake's Island shows clearly, however, that there is such a difference. If we take the ratio of the amount of growth in the males to that in the females in each millimetre group at each period of collection, and from this obtain a mean value for each period, we get the results which are shown in Table I (p. 730).

Excepting the first month when the amount of growth was so small as to be difficult to measure, and therefore not very reliable, there is in all cases a definitely greater rate of growth in the females than in the males.

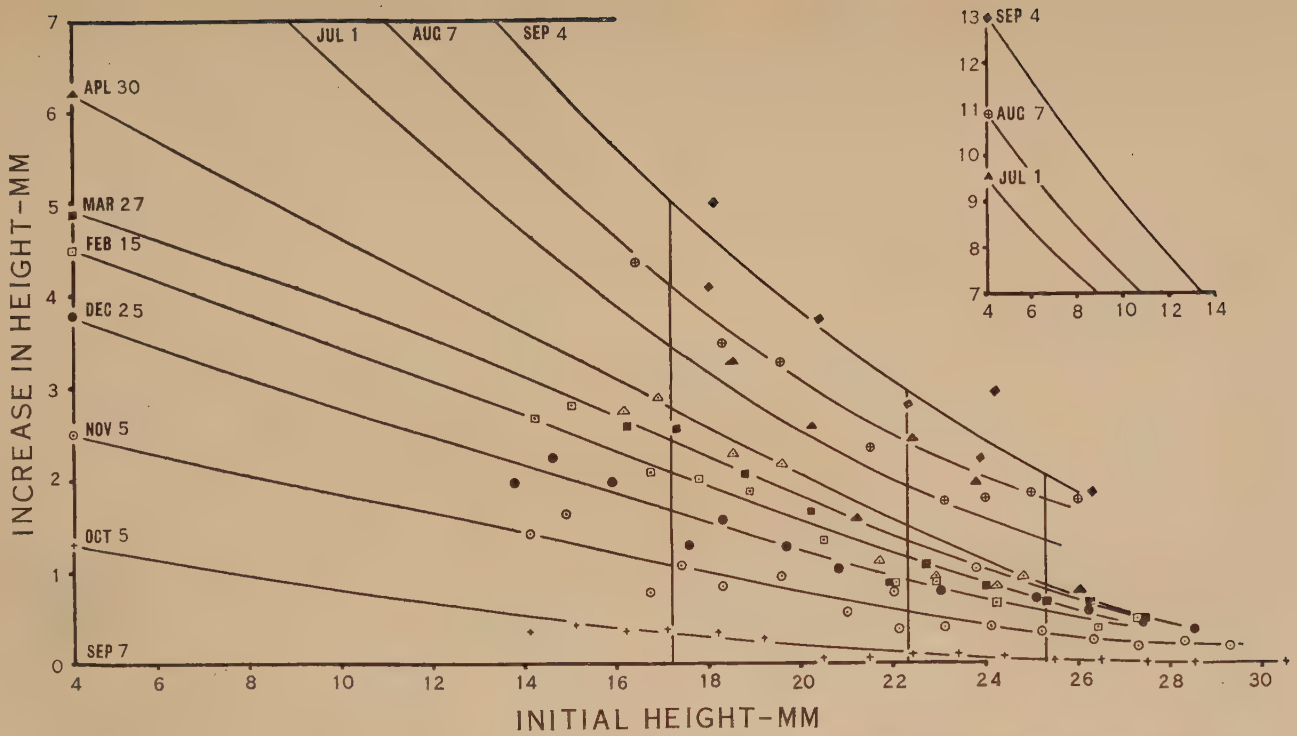


FIG. 5.—Growth of marked *L. littorea* at successive intervals of measurement on Drake's Island. Each point represents the mean for all individuals commencing growth within a given millimetre group.

A greater growth-rate in females than males has been indicated in the case of two Indian Littorinas also, *L. scabra* and *L. obesa* (Sewell, 1924). On the other hand there is a suggestion of a greater rate of growth in the males of *L. littorea*, at any rate in their first year, made by Linke, who says (1933, p. 4): "Auch die Jungen von *L. littorea* werden erst nach einem Jahr geschlechtsreif, das Männchen hat dann eine Schalenhöhe von 13 mm., das Weibchen eine solche von 8 mm. (Pelseneer, 1926)." This appears, however, to be a misunderstanding of Pelseneer's statement (p. 18): "Je dois faire remarquer que ce pénis n'est d'ailleurs jamais développé avant que les individus considérés aient comme dimension 13 millimètre de hauteur de coquille, alors que, pour un hauteur de 8 millimètres, des ovules sont déjà reconnaissables dans la glande génitale des ♀♀." Such a differential growth-rate explains the preponderance of females over males found in the larger sizes. Pelseneer (1926), in an examination of 516 individuals of from 13 to 15 millimetres in height, found 50·96% of females, as compared with 67·18% of females in a sample of 192 individuals over 2·2 cm. in height. Table II shows a similar condition at Trevol, the males and females being present in about equal proportions up to a height of 25 mm., after which the proportion of females rises rapidly to three-quarters of the population. Sewell found a similar result with the Indian species.

TABLE I.

Date.	Ratio of ♂ : ♀ growth since Sept. 6, 1934.	Number of specimens.
Oct. 5 1934.	(1·48 : 1)	131
Nov. 5	0·90 : 1	145
Dec. 10	0·82 : 1	334
Jan. 9 1935.	0·98 : 1	61
Feb. 15	0·83 : 1	97
March 27	0·91 : 1	76
April 30	0·84 : 1	84
July 1	0·60 : 1	17
Aug. 7	0·68 : 1	30
Sept. 4	0·52 : 1	12

There are practically no data available which allow of the comparison of the growth-rate of *L. littorea* at Plymouth with that in other localities. Wright (1936) has published figures for growth in the Blackwater estuary in Essex, which show a height in December of their first year of about 8 mm., and a height of about 12 mm. the following April. But his further figures of 21–22·5 mm. in October of the second year, and 23 mm. the following April when the winkles are practically two years old are read from size-distribution peaks which are most probably multiple, and which are based on the wholly inadequate numbers of 19, 44 and 7 individuals respectively. Hayes (1929) gives some figures for growth over a short period at St. Andrews, N.B., which showed a progressive decrease in growth-rate of adult winkles with increasing height above low water.

TABLE II.

Mean height. mm.	% of ♀♀.	No. of specimens.
15·8	47·5	202
16·8	50·0	214
17·8	46·3	317
18·8	54·6	317
19·8	50·9	320
20·8	48·1	318
21·8	45·1	315
22·8	42·6	317
23·8	51·7	311
24·8	48·7	288
25·8	59·0	251
26·8	68·9	106
27·8	77·8	36
29·8	76·9	26
	Total	3338

Shell Shape and Weight.

Shell shape in *L. littorea* shows very much less variation from one locality to another than in *Purpura lapillus* (Moore, 1936), this being probably associated with the dispersal obtained by the pelagic eggs of the former, the young Purpura hatching and dispersing on the same ground as the adults. The spiral angle α (Moore, 1936, p. 72) appears to remain more or less constant up to a height of 1–1·5 cm., and thereafter to drop fairly steadily. The value for the small shells was about 82·6°, and the lowest value observed in large shells was 81·1°. The apical half-angle θ appears to rise slightly to a maximum at a height of about 1–1·5 cm., and, as in α, to fall steadily with further increase in height. Table III shows the values of α and θ at a height of 2·0 cm.

For a given height of shell, an increase in apical angle will tend to result in an increase in the shell weight, but since an increase in the spiral angle will tend to reduce the weight, and since these two angles vary in the same direction with increasing shell height, the weight does not show any great departure from a linear relationship with the cube of the height.

TABLE III.

Locality.	α	θ
Trevol	32·4°	82·46°
Hannafore Point, Looe .	40·8°	81·95°
Polperro	38·9°	82·30°
Wembury, Church Reef .	40·4°	82·08°
Charlestown . . .	38·8°	81·72°
Drake's Island . . .	41·4°	82·10°

Fig. 6 shows the shell weight -height relationship for the three Plymouth grounds. In *Purpura lapillus* a close correlation was found between sexual maturity and the changes in the fundamental shell angles, but this is not apparent in *L. littorea.*

MATURATION OF THE GONADS AND SPAWNING.

The anatomy of the gonads and genital apparatus has been described in detail by Linke (1933), and on pp. 38–40 he summarized the information extant on the eggs and the process of laying them. According to him spawning takes place in March, April and May, though in extreme cases there may be some spawning as early as January and as late as June; and he states further that eggs of *L. littorea* have been found in the plankton as early as November. Spawning takes place chiefly on the flood tide and at night. Elmhirst (1923) gives the spawning season at Millport as January to July and rarely August, and states that young appear abundantly on the shore by April. Tattersall (1920) gives the breeding season as January to June with a maximum in April and early May, and states that the males become mature in early January, but that he did not find any females with the ovary ripe until the middle of February. He found spent males after the beginning of April.

The results obtained from gonad examinations of winkles from Trevol are very similar (Fig. 7). No ripe females were found before early February, but between then and mid-March spawning took place rapidly, although some females not yet completely spent were still to be found at the end of May. No fully ripe males were recorded before the beginning of January, but at that time most of the males contained a certain number of apparently ripe sperm, and were presumably capable of copulating. By early February all the males were fully ripe, and in May a few spent ones were found. The curves showing the seasonal variation in tissue weight on the different grounds (Figs. 8, 9, 10) indicate similar results, if the spring drop in weight is taken to represent loss due to spawning. At Trevol and Drake's Island the spawning appears to commence about the beginning of December, and at the Yealm perhaps slightly earlier, although no sample was taken there in December. At Trevol, where the tissue weights of the males and females were determined separately, the males show a drop in weight commencing about a month before the females, that is at the beginning of November, this earlier loss of weight being no doubt due to copulation which precedes spawning by a variable period. On all three grounds spawning appears from the tissue weight figures to have been practically complete by some time between mid-March and mid-April. Dr. M. V. Lebour's observations on the occurrence of the eggs and larvae of *L. littorea* in the plankton

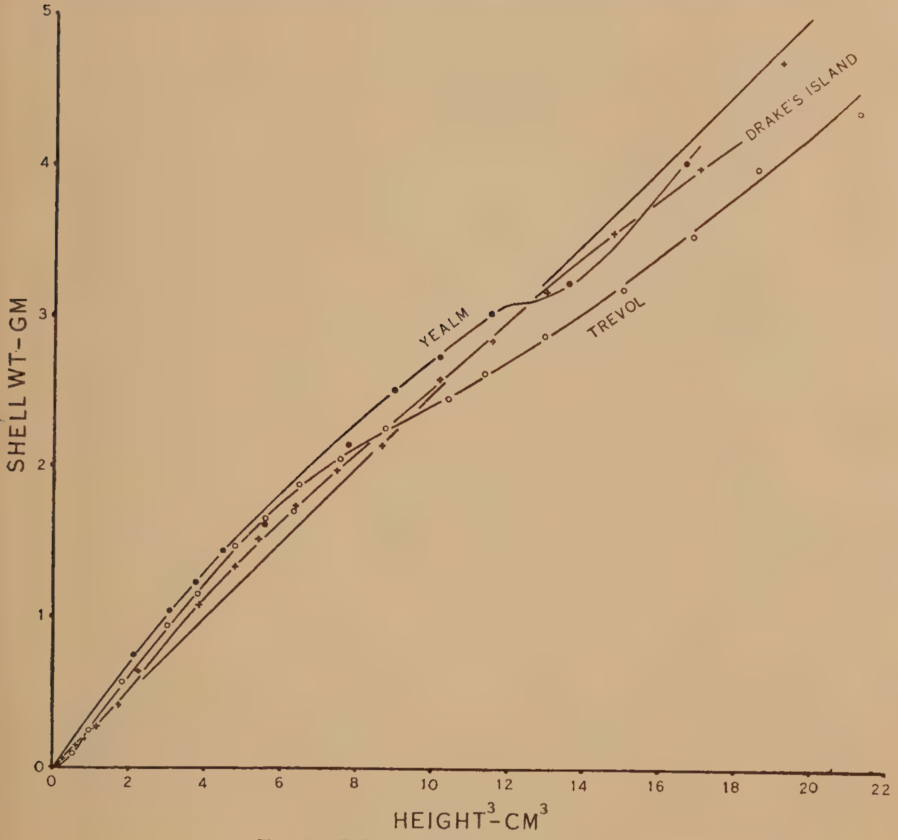


FIG. 6.—Relation of shell weight to height.

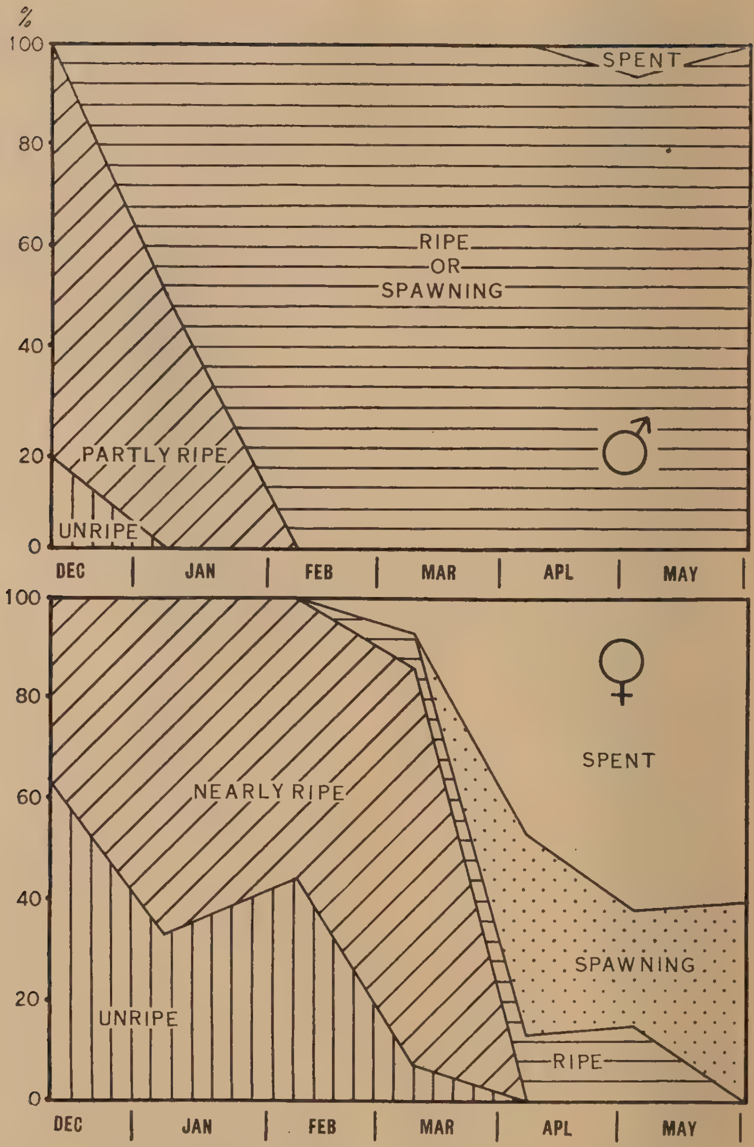


Fig. 7.—Gonad condition of *L. littorea* at Trevol in 1935–36.

round Plymouth, confirm these dates. She says (personal communication) that the first eggs are usually seen about the middle of November, and that a few may be taken as late as June, but that the greatest numbers are in February and March. With regard to the time of settlement of the young on the shore, the 1935 brood was specially searched for with a fine sieve at Trevol on May 17 of that year and none were found, but at the next visit on July 1 they were abundant. At Drake's Island the 1936 brood was not found on the shore on April 21, and was recorded as present, but not plentiful on May 19. On June 2, 1936, they were present in very small numbers only at Trevol. About the end of May to the end of June may therefore be taken as the main period of settlement of the young on the shore, and if this is so Elmhirst's statement of the abundance of newly settled young on the shore in April is open to question.

Fig. 8 shows a curve for mean monthly temperatures for the sea off Promenade Pier, Plymouth, for the years 1912–19 (Orton, 1920), and from this it will be seen that, if we take the spawning period as falling in the months February to mid-April, the corresponding sea temperatures will be from the winter minimum of about 8° C. to an upper limit of about 9° C., with a small amount of earlier spawning on a dropping temperature from about 10° C. downwards.

TISSUE WEIGHTS.

The tissue weight curves in Figs. 8, 9 and 10 were obtained as follows : From all three grounds, curves were available relating tissue weight to shell height, at intervals through the year (p. 723). Curves showing shell growth during the first two years of life, as indicated by the size distribution curves, were also available for all three grounds, and for Drake's Island the growth during subsequent years could be calculated from Fig. 5. The shell height curves were therefore drawn, using the cube of the height as being likely to have an approximately linear relation to weight, and the observed tissue weights then inserted for the shell heights corresponding to the successive seasons of sampling. As shell-height curves for only the first two years were available for the Yealm and Trevol, their subsequent growth was assumed to be similar to that at Drake's Island, but less throughout in the ratio of $\frac{\text{height (Yealm)}^3}{\text{height (Drake's I.)}^3}=0{\cdot}46$ for the Yealm, and greater for Trevol in the ratio $\frac{\text{height (Trevol)}^3}{\text{height (Drake's I.)}^3}=1{\cdot}22$ these being the observed ratios on the last dates on which accurate figures are available from size distribution curves, namely, November 11 (2nd year) for the Yealm, and July 30 (2nd year) for Trevol. It is fully realized that such figures for the third and subsequent years are only

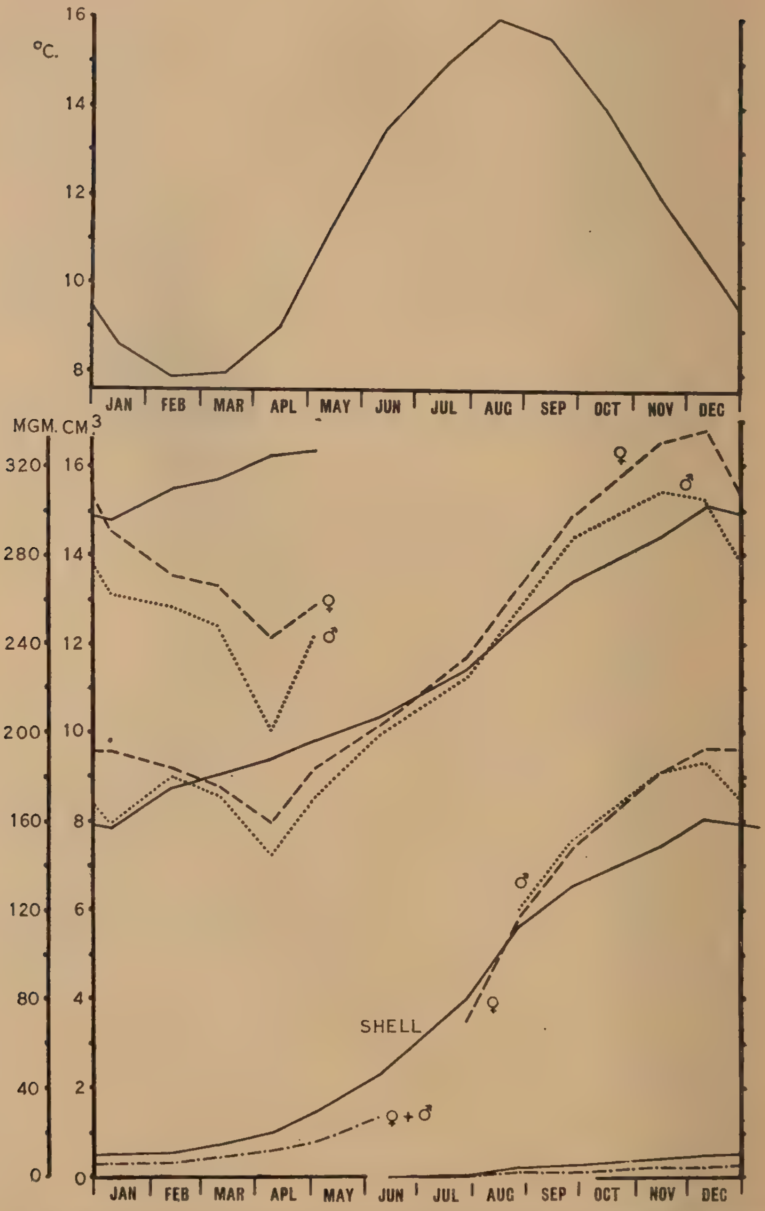


FIG. 8.—Monthly mean sea temperatures for Plymouth (1912–19); growth of the shell (height^3) and of the tissues (dry weight) in the successive year-groups at Trevol.

rough approximations, but the purpose of the tissue weight curves is not to show the absolute tissue weight at any given time, but rather to show its seasonal variation, and the degree of this variation at different ages relative to the shell size, and to show also the differences, if any, in the seasonal variations in tissue weight in the two sexes. For this the shell heights used form an adequate framework. Separate data for the males and females are available only from Trevol, and even there only above an age of one year, the sexes not having been found separable externally in the younger stages. No account has been taken of the observation that the females grow somewhat faster than the males,

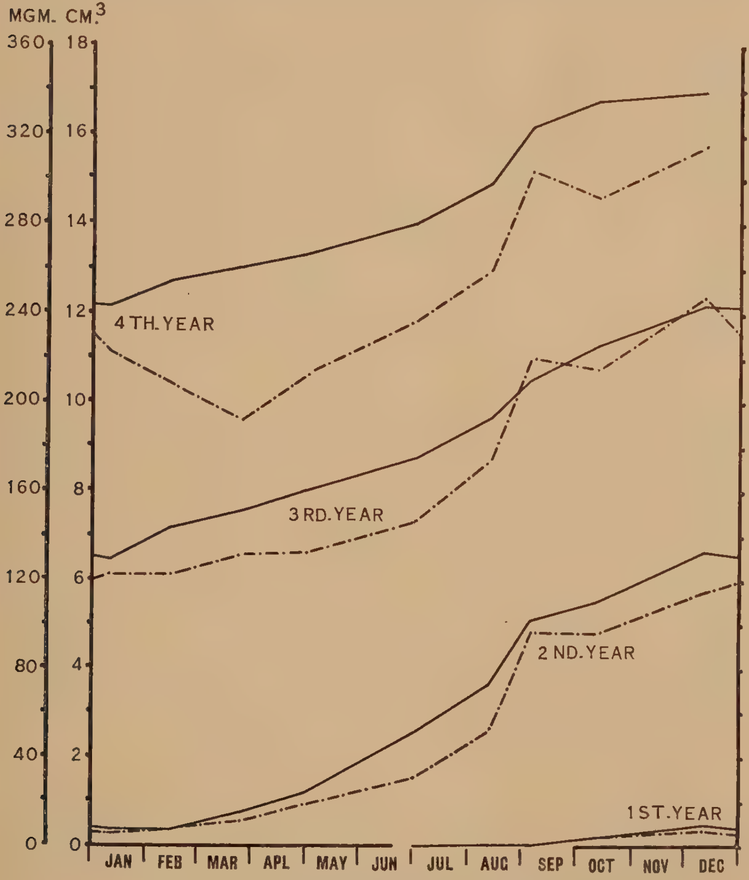


Fig. 9.—Growth of the shell (height^3) and of the tissues (dry weight) at Drake's Island.

since it would only have added complexity to the diagrams, but if the difference in growth of the two sexes is the same at Trevol as it is at Drake's Island, then it may be taken that the tissue weights for the females should be about 10% greater, and those for the males about 10% less throughout than those shown. This, however, has no effect on the general deductions drawn from the graphs.

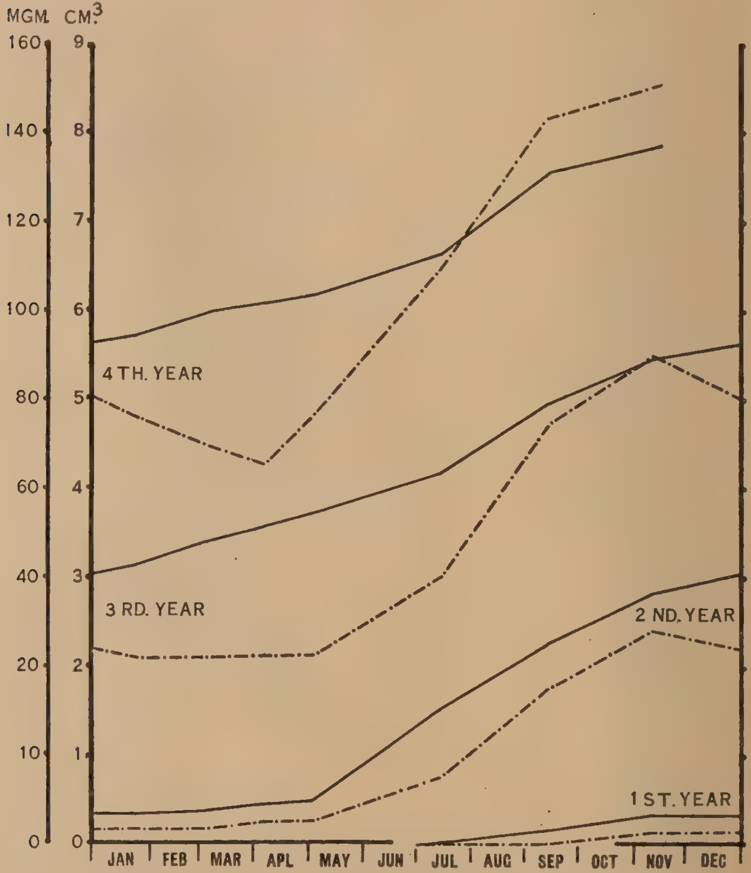


Fig. 10.—Growth of the shell (height³) and of the tissues (dry weight) at the Yealm.

The relatively slow growth-rate of the Yealm winkles is rendered even more noticeable when, instead of being recorded in terms of height, it is shown in the more natural units of either tissue weight or height³. It is then seen that the growth at the Yealm is only about half that of Trevol and Drake's Island. In shell growth then, Drake's Island and

Trevol are more or less similar, in contradistinction to the Yealm. With regard to tissue growth, however, there is a point in which Drake's Island and the Yealm differ markedly from Trevol. It was found by examination of samples of winkles from Drake's Island in December, 1935, and from Trevol and the Yealm in March, 1936, that on all grounds the 1935 brood, which were then 3–6 months old (since settling), were immature sexually, while the 1934 brood, then 15–18 months old, were all definitely mature. The tissue weight figures for Trevol confirm this, showing a marked drop in weight in the second spring, indicating presumably a considerable spawning when 18 months old, but on the other two grounds, and in particular on Drake's Island, there is indication of very much less spawning, and it is not until the winkles are 2½ years old that the loss of weight at spawning is really marked, and even then the weight loss is not as great as it is at a corresponding age at Trevol. The latter locality therefore appears to be markedly superior to the other two so far as production of larvae is concerned.

MORTALITY RATE.

The size distribution curves in which it is possible to separate the numbers of shells in the first, and sometimes also the second year groups from those of all older groups, allow of the calculation of the rate of mortality in those groups. This is, of course, possible only if the sample is an adequate one so far as those groups are concerned. After the shells are about one centimetre in height, the sampling may be taken to be adequate on all grounds. With the method of sampling used at Trevol, the first year groups also may be taken to be adequately sampled there from the spring of 1935 on. The method also assumes that the spat-fall is similar in different years. While this is almost certainly not strictly true, yet the general impression obtained is that the wide fluctuations observed in the spat-fall in different years in many lamellibranchs does not occur in this species, and that one year is substantially similar to another, at any rate in this region.

At the time when the young post-larval winkles are settling on to the shore, the loss by death will be to some extent counteracted by gain from the plankton so that the mortality rate cannot be estimated by this method, but by the end of July the gain from the plankton may be assumed to be negligible. In the two samples from Trevol on July 30 and August 28, 1935, the ratios of the numbers of 1935 group shells to all older ones was 8·6 : 1 and 8·4 : 1 respectively. Taking 8·5 : 1 as the mean value, then out of every 950 shells of all ages at that time, 850 are first year, and 100 are in their second or subsequent year. Of these hundred, $100\times\frac{1{\cdot}4}{2{\cdot}4}$ or 58 are in their second year (1·4 : 1 is the ratio in the second and subsequent years, see below). That is to say that, if the July–August rate were maintained for a year, only 58 animals would survive out of an initial 850 newly settled young. This gives a mortality rate of 94 per cent per annum for the months July and August, but if during this time there was any further settlement from the plankton, then the rate must be even higher, and during the period immediately after settlement the rate almost certainly is higher. It seems desirable to omit the samples in September, 1935, and in May, 1936, as being obviously not representative. Doing this, and working out the ratio of the 1935 group to all older shells for all samples from Trevol from September, 1935, to June, 1936, the mean value for the ratio comes to 1·7 : 1, and similarly, taking the mean value of the ratio of numbers in the 1934 group to all older ones in the period July, 1935, to June, 1936, the result is 1·4 : 1. The ratios therefore drop from 8·5 : 1 in the first few months, through 1·7 : 1 for the remainder of the first year to 1·4 : 1 in the second year, and this may probably be taken as a mean figure for all older shells also. Translating these ratios into percentage mortalities, the results are 94 per cent per annum or more for the first two months, 66 per cent for the rest of the first year, and 57 per cent thereafter. Sampling on Drake's Island was less adequate, and a figure can be obtained for the second and subsequent years only, the ratio here being 1·85 : 1, corresponding to a mortality rate of 65 per cent, which, within the limits of experimental error, may probably be taken as about the same as at Trevol. At the Yealm the results are extraordinarily different. The mean value of the ratio here for the 1935 group for the period July, 1935, to March, 1936, was 0·92 : 1, corresponding to a mortality rate of 82 per cent per annum, while for the older individuals of 15 months old and more, the mean value was 0·30 : 1, or only 23 per cent per annum.

Although these are only approximate figures, the difference between 23 per cent at the Yealm and 55–65 per cent on the other two grounds is too large not to be significant. It cannot be accounted for by collecting by fishermen, since such little collecting as there is takes place at Trevol and the Yealm, and not on Drake's Island. The only internal enemies known to have any serious effect on winkles are cercariae, and for these Rees's figures (1936, p. 358) show a total infection for all species of cercariae of only 10 per cent at Drake's Island and 2 per cent at Trevol. Even if the Trevol percentage is rather low, it is far too small to account for the observed mortality, and none of the cercariae are, according to Rees, likely to be fatal to the winkle, the only definitely fatal species, *Cercaria emasculans*, not having been found on these grounds. It must, however, be noted that among very large winkles the percentage infection by cercariae is much higher. At Aberystwyth (Rees, 1935) the total infection by all species in winter was 4–5 per cent, probably somewhat more in summer, and *C. emasculans* accounted for only about a third of this, so that there also it would be a negligible factor in the general mortality. We are forced therefore to look for either a limiting environmental factor or enemies such as birds or fish which might kill the winkles in considerable numbers, and at present the available information on these is very scanty.

SUMMARY OF CONDITIONS ON THE THREE GROUNDS.

	Trevol.	Drake's Island.	Yealm.
Level.	Mid-tide.	Mid-tide to between mean low water of neaps and springs.	Mean low water of spring tides.
Habitat.	Mud.	Stones.	Stones.
Growth-rate.	About the same as on Drake's Island.	Hts. (mm.) ½ year . 14·0 1½ years . 17·4 2½ years . 22·4 3½ years . 25·4 4½ years . 27·3	Much less than on Drake's Island.
Yearly variation in growth-rate.	Growth-rate progressively less in 1934–35–36.	Growth-rate progressively greater in 1934–35–36.	Growth-rate approximately the same in 1934–35 (–36?).
Age at sexual maturity.	18 months.	18 months.	18 months.
Age at first considerable spawn output.	1¾ years.	2¾ years.	2¾ years.
Mortality rate.	57%	65%	23%

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The Development of the Hydroid *Corymorpha nutans* M. Sars from the Egg.

By
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With 2 Figures in the Text.

During the summer of 1936 I obtained mature specimens of the medusa* of *Corymorpha nutans* at Plymouth. An account of the early development of the hydroid reared from the fertilized eggs of these is given below. Young polyps of this species have been figured by Allman (1871) and by Hartlaub (1907). Allman found his young polyps developing apparently from the rooting filaments of the parent hydroid which had become free. Hartlaub figures and assigns young polyps which he found in the plankton at Helgoland to this species.

A large number of medusae were captured off the Eddystone on May 18th, 1936. These were isolated overnight in a finger-bowl of sea-water. Next morning several of the medusae which were ripe had shed their sexual products. Such medusae were disintegrating, although others in the same bowl but not quite ripe were quite healthy and swimming actively. Both healthy and disintegrating medusae were removed by pipette. Left on the bottom of the bowl were a number of large opaque eggs easily visible to the naked eye. When observed they had evidently been fertilized and had a distinct yellowish pellicle around them. None had hatched on May 21st, but by May 25th a number of young had emerged and others were emerging (Fig. 1, A–D).

These liberated eggs measure from 0·26–0·28 mm. in diameter. Eggs obtained from mature medusae on May 26th exhibited activity and movement and these are figured (Fig. 2, A–F). The pellicle of the egg is very elastic and is pushed out into broad pseudopodial-like growths on the under side into contact with the substratum to which the pellicle adheres. The so-called "pseudopodia" then withdraw into the main body and the dilated pellicle shrivels up into a small tube. Several of these may be formed (Fig. 2, F) and they anchor the egg to the substratum. They may be termed anchoring filaments.

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* *Steenstrupia* (*Corymorpha*) *nutans* of the Plymouth Marine Fauna. For a description of this medusa see Browne (1896).

The young developed directly out of the eggs into young polyps instead of emerging as ciliated planulae which is the more usual way of development among hydroids. In this respect it resembles *Corymorpha palma* Torrey, 1902 (see Torrey, 1907). According to Torrey, however, the larva of *C. palma* emerges from the egg-case and wanders aimlessly about before settling down. My specimens were very inactive and the young hydroids grew out of the egg-cases and proceeded to differentiate into hydrocaulus and hydranth, the latter developing tentacles. The proximal ends of the hydrocauli were still inside the egg-cases in the majority of the specimens and would probably have remained so if the bowl had been undisturbed. The proximal ends of the young polyps, however, were not attached in any way to the egg-case.

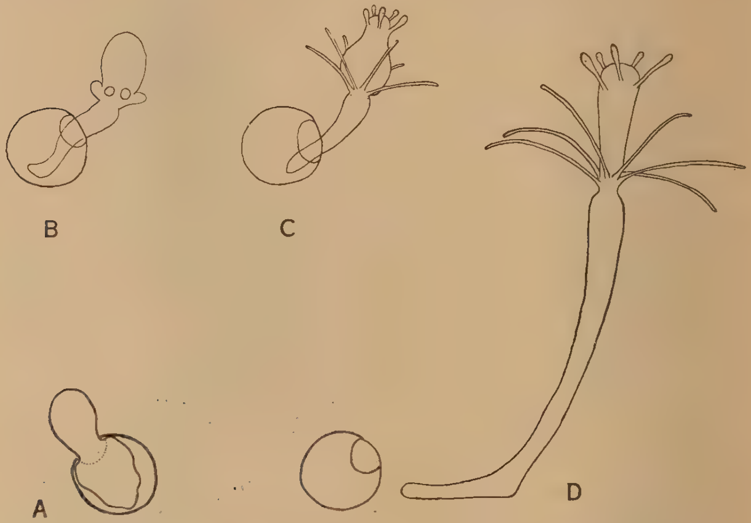

Fig. 1.—A–D, various stages of development of young polyps of *Corymorpha nutans*; Plymouth, 25.v.36.

Young polyps taken on May 26th possessed 4–6 oral tentacles and 6–8 aboral tentacles. The measurements of a typical young hydroid at this age are given below :—

Maximum length of hydrocaulus	1·6 mm.
Maximum diameter of hydrocaulus	0·14 mm.
Diameter of hydranth	0·3 mm.
Length of oral tentacles	0·12 mm.
Length of aboral tentacles	0·5 mm.

After another week one of the polyps had developed 8 oral tentacles and 15 aboral tentacles. By this time, June 3rd, the young polyps had developed rooting filaments (the "frustules" of Allman) on the proximal part of the hydrocaulus. They were always few in number and each consisted of a fine filament with a clavate tip by means of which the polyps attached themselves to the substratum. After secreting a thin perisarc around itself the protoplasmic connexion with the hydrocaulus breaks down and eventually disappears, leaving the perisarc as an empty anchoring filament. The formation of this filament and its subsequent development appears to be identical with the process described by Torrey (1907) for *C. palma.*

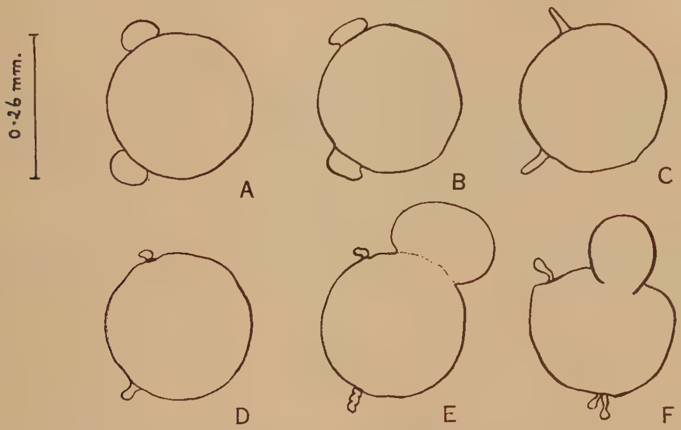

Fig. 2.—A–F, movements shown by a single fertilized egg of *Corymorpha nutans* during thirty minutes; Plymouth, 26.v.36.

On June 23rd the single polyp left in the bowl developed the rudiment of a gonophore stalk on the body of the hydranth on the distal side of the aboral tentacles. During the next few days the rudiment became divided but did not develop further. At this age the polyp possessed 15 oral and 17 aboral tentacles and a distinct, firm, brownish pellicle. The pellicle, however, was present on one of two polyps on June 3rd as a very thin, delicate membrane. The development was not studied further.

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On a Remarkable Process of Bud Formation in a Gymnoblastic Hydroid (*Heterostephanus* sp.).

By

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With 3 Figures in the Text.

THE process of asexual reproduction described below, is, as far as the writer is aware, unique among hydroids. In all known species of hydroids in which an asexual bud formation has been described (e.g. in *Hydra*), the mouth and oral tentacles develop at the free end of the bud and the proximal or fixed end becomes the base. The sequence of development of medusa buds is essentially similar. This method applies also to budding in other Coelenterates. In the present instance the bud instead of growing out "head first," came off "tail first"—the proximal end developing mouth and oral tentacles and the free end becoming the stalk. I can find no record of such a method having been described before.

The hydroid on which it occurred was dredged from below low-water mark near the eastern end of the Plymouth Breakwater. The polyp was found on a piece of hapteron (the so-called "root") of *Laminaria cloustoni* on July 9th, 1936, that had been allowed to stand in sea-water for two days. When first observed the polyp was in a very contracted condition, so it was picked off the hapteron and removed to another bowl for a further period of two days.

On July 14th the hydroid was seen well expanded (Fig. 1). It consisted of a solitary polyp bearing some resemblance to a young polyp of *Corymorpha nutans* M. Sars, 1835, having oral and aboral tentacles. It differed from this hydroid in that the four oral tentacles were capitate and the eight aboral tentacles were moniliform; the latter in two closely approximated whorls of four long and four short ones. The longer tentacles carried 10–12 batteries and the shorter 6–7 batteries of nematocysts completely encircling the tentacle. Both tentacles and the stalk were very contractile, capable of expanding to five times their contracted length. The posterior end of the hydranth carried four backwardly directed papillae. The stalk was covered by a membranous hyaline perisarc. The total height of the polyp was 3 mm.

On July 17th a swelling appeared on the body of the polyp at the level of the longer whorl of tentacles carrying outwards with it one of the long tentacles. On the next day this swelling was clearly seen to be some kind of "bud." Small processes, four in number, appeared on the level of the long tentacle (Fig. 2). At this stage the number of nematocyst rings on some of the tentacles of the parent polyp had increased. One long tentacle now possessed fifteen rings and a shorter tentacle had eight.

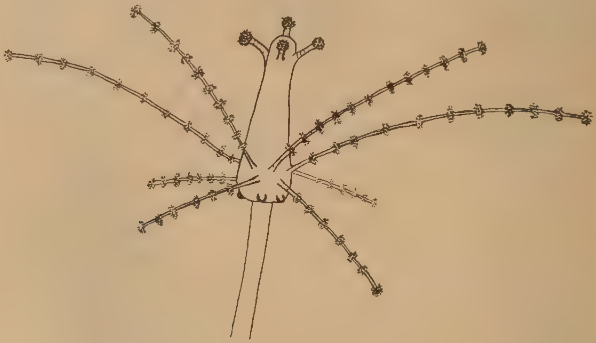

FIG. 1.—*Heterostephanus* sp., from the hapteron of *Laminaria cloustoni*, hydroid fully expanded with part only of the hydrocaulus shown; Plymouth, 9.vii.36.

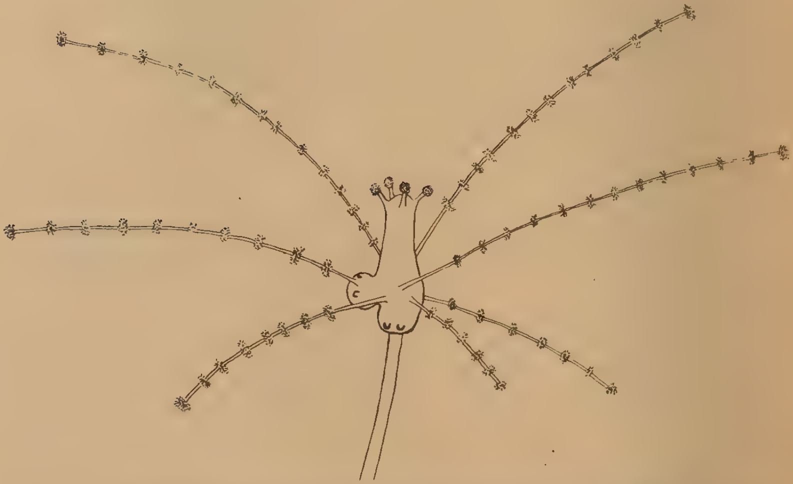

FIG. 2.—*Heterostephanus* sp., first stage of the formation of the bud (lower part of the hydrocaulus not shown); Plymouth, 18.vii.36.

Two days later the bud had grown in size and its free end had become transparent and pointed. The four processes already noted had grown

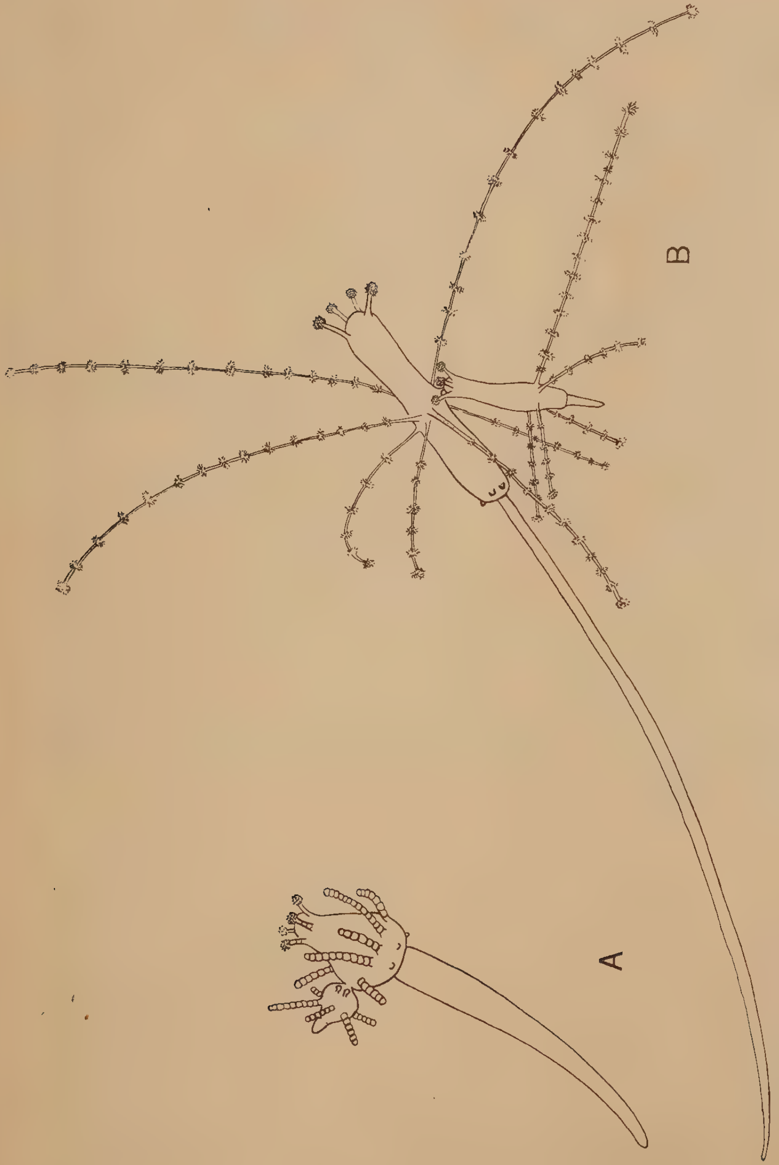

FIG. 3.—*Heterostephanus* sp.: A, hydroid contracted showing aboral tentacles and rudiments of oral tentacles; Plymouth, 20.vii.36: B, bud fully formed but still attached to parent polyp; Plymouth, 21.vii.36.

out into short annulated tentacles each with 4–6 rings. Small processes were also observed developing near the point of attachment of the bud (Fig. 3, A).

Next day (July 21st) the bud had elongated considerably. The small processes noted the previous day had developed into four capitate tentacles (Fig. 3, B). The free end had become quite distinct and resembled the stalk of the parent. On the same day the bud broke away and quickly settled down on the bottom of the bowl, attaching itself within thirty minutes of becoming free. Before nightfall, the stalk had elongated considerably (to about half the length of the stalk of the parent). Both polyps died on July 23rd, probably due to overfeeding.

On September 29th a second polyp was found among some fine gravel from the Eddystone by Dr. M. V. Lebour, who kindly gave me the polyp for examination. When found it was in a much contracted condition, but by next day it was fully expanded and could be definitely recognized as belonging to the same species as the one which I had previously found. The hydranth was brownish in colour and possessed four oral capitate tentacles and four long and two shorter aboral tentacles. The membranous perisarc was distinct and of a slightly brownish colour and better developed than in the first polyp found. At the posterior end of the hydranth there were four papillae directed backwards. The length of the hydranth expanded was 1 mm., the length of the hydrocaulus when expanded was 1·4 mm. and 0·45 mm. when contracted. The polyp lived only three days after it was found.

While the bud-formation described above may probably be the usual way of asexual reproduction in this species, the carrying away of one of the parent polyp's tentacles is perhaps not typical but depends on the point of origin of the bud.

SYSTEMATIC POSITION.

This hydroid appears to be closely related to the genera *Rhizotrichia* Stechow, 1919 (=*Trichorhiza* Russell, 1906), *Heterostephanus* Allman, 1864, *Acharadia* Wright, 1863, and *Vorticlava* Alder, 1857. It is distinguished from Acharadia and Vorticlava by its aboral tentacles being annulated with clusters of nematocysts ; from Rhizotrichia by its simple undivided hydrocaulus and by the possession of only four oral capitate tentacles. It appears, however, to be more nearly related to *Heterostephanus annulicornis* (M. Sars, 1860). It seems to differ from this last species in having only four oral tentacles, fewer aboral tentacles, in its thin perisarc, much smaller size and delicate appearance. All these differences may be due to age and growth and my specimens may possibly be young hydroids of *H. annulicornis*. Until knowledge of the gonosome of my species is obtained I do not feel justified in assigning it to *H. annulicornis* or to any other species and simply place it provisionally in the genus *Heterostephanus* Allman.

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Notes on the Culture of some Marine Plankton Organisms.

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In recent years considerable advance has been made in the methods for culturing marine organisms. We are still unable to dispense with sea-water as the main component of the culture medium, and in this respect, in spite of some notable efforts (Allen, 1914), the methods are less satisfactory than those developed for many freshwater organisms and based on synthetic media (Hartmann, 1928; Belar, 1928; Pringsheim, 1924). But the application of certain standards of purity and sterility in medium, culture dishes and instruments to culture work on marine organisms (Allen and Nelson, 1910), the enrichment of sterilized sea-water with certain nutrient salts (Allen's modification of Miquel, Schreiber), and more recently the development of the "Erdschreiber" as a culture medium (Föyn, 1934) have made possible the culture of an increasing variety of marine protozoa, algae and small invertebrates. In the last-mentioned medium Föyn cultured the algae Ulva and Cladophora, and Hämmerling (1934) two species of Acetabularia through several generations; the present author used it for Artemia, the brine shrimp (1932), and for Noctiluca (1934); Hartmann and Huth (1936) for Ophryotrocha, Shen (1936) for Dinophilus and Rühmekorf (1935) for a hypotrych ciliate, Keronopsis. Growing Ulva and Cladophora from parthenogametes of a single plant in six different media, under otherwise very similar conditions, Föyn showed that the media could be arranged in the following order of quality: pure sea-water——>Schreiber's medium——>Allen's medium——> Killian's medium——>sea-water+soil extract——>"Erdschreiber."

Since autumn, 1935, I have been studying chiefly the life-histories of certain plankton diatoms, an account of which will be published elsewhere. In the following pages a short description is given of the culture technique developed for the centric diatoms which may be of some value for future investigators. Notes on the culture of certain other plankton organisms are included, and on attempts to rear fish larvae which failed but gave some indication of how such rearing might in future be undertaken with more success.

CULTURE METHODS FOR DIATOMS.

Föyn's "Erdschreiber" is a combination of Schreiber's medium (Schreiber, 1927) and soil extract, which has been used before for the culture of freshwater algae (Pringsheim, 1924). It consists of :—

$NaNO_3$	0·1	g.
Na_2HPO_4 . . .	0·02	g.
Soil extract . . .	50	c.c.
Sea-water . . .	1000	c.c.

The soil extract is made up by boiling for one hour 1 kg. of good garden or potting soil with 1 litre glass distilled water in an autoclave. (More recently I have been using tap water with equal success.) After 2–3 days the resulting brown and rather dirty fluid is decanted into a flask and sterilized by heating up to the boiling point. After standing for 3–4 weeks the rougher particles settle to the bottom and the fluid becomes transparent, brown or red in colour and ready for use. If mould or bacteria develop in the meantime it must be sterilized again. In any case, repeated decanting and boiling enhances the process of clarifying the fluid. Before use the soil extract is poured into another flask and boiled for a short time ; the required amounts of nitrate and phosphate are then dissolved in it and sterile sea-water added. If large quantities of culture medium are needed at short intervals one or more litres of soil extract with the nitrate and phosphate already dissolved can be kept in stock, and the culture medium quickly made up with sea-water before use. It is advisable to keep the stock solution in a refrigerator and to avoid boiling the soil extract once the salts had been added.

Throughout the work "outside" sea-water* has been used. It was first filtered through filter paper (Whatman No. 1) and then heated to boiling point. Since boiling produces some physico-chemical changes it is advisable to allow this water to stand for 3–4 weeks before use. During this period the sea-water recovers its normal O_2 and CO_2 content and the pH returns to its normal value (Schreiber, 1927). If no old sterile sea-water is available fresh sea-water should be filtered and heated only to 70° C. The flasks with soil extract, sea-water and culture medium should be closed with overlapping glass capsules. Paper bound with string round the top and neck of the flasks is useful for keeping the dust off the glass capsules.

Small watch glasses, 5 cm. in diameter, with ground edges, containing about 2 c.c. of fluid and covered with round glass plates, and Petri-dishes about 10 cm. in diameter, were used as culture dishes. These as well as the flasks for sea-water and culture medium, the glass capsules and pipette tubes—in short, all glass ware for culture purposes—were first cleaned by being either put into or filled with a mixture of sulphuric acid-bichromate for several hours. Then they were thoroughly rinsed with tap water and finally the smaller glass ware was boiled in a porcelain dish with glass distilled water, and the flasks filled with a small amount of distilled water and boiled over the gas burner.

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* At Plymouth the water from the Sound or in the Aquarium circulation is too contaminated for delicate organisms and water is therefore collected in the open sea well outside the Breakwater ; this is called "outside" sea-water.

The greatest difficulty confronting the culturing of marine unicellular algae is to start the culture free from flagellates and bacteria. Allen and Nelson (1910) often succeeded by diluting a small quantity of a plankton sample containing diatoms, or colonies of a species developed in a raw culture, in a large quantity of culture fluid and subdividing it into a number of culture flasks. Schreiber used a special apparatus, the "plankton purifier."

In my own experience the direct method, that is the isolation of a few or single cells from a plankton sample, gave quick and satisfactory results. The diatoms were isolated under a low-power binocular dissecting microscope from catches with a very fine silk tow-net. This dissecting microscope is the most important piece of apparatus for culture work. Even for the smallest plankton diatoms the combination of the eyepieces ×8 and the objectives ×3, ×4 and ×8 gives a range of magnifications sufficient not only for isolation, washing and subculturing of the cells, but also for the study of the division rate, and control of the general health of the diatoms, of the appearance of resting-spores or auxospores, and even of the presence of infections by very small flagellates. It is only for ensuring purity from bacteria that one has to use the high-power microscope.

The diatoms were picked out singly with fine pipettes. It is important to take the cells out with as little fluid as possible to avoid contamination. For this purpose the fine end of the pipette should be long (about 5 cm.) and of a more or less uniform diameter with an opening not exceeding twice or three times the diameter of the cell to be isolated. The cell drawn into the pipette is then squirted sharply* into a watch glass with 1–2 c.c. of sterile culture medium. If left in this watch glass for a few days the cell might divide and give rise to a colony, but small flagellates would almost invariably develop and eventually overgrow the diatoms completely. It is therefore essential to wash the isolated cells by passing them through a further 2 or 3 sterile water samples in watch glasses. Working with the lowest possible magnification it does not take long to find a single diatom cell in a volume of 1–2 c.c. of water. Next day if the diatoms are in a healthy state they have either divided or grown in size or are suspended in the water, in short, they show a definite improvement as compared with their usually lethargic state in the overcrowded townettings. The washing is repeated once or twice and the cells left for a few days in a watch glass, well covered with a glass plate. If they reproduce satisfactorily a sample may be washed after a week or so and transferred into a Petri-dish. In spite of a good initial growth of the diatoms the subsequent cultures must be carefully watched for the presence of small flagellates. The reproduction of these may at the beginning be inhibited by the growth of the diatoms, particularly if the light and temperature conditions are very favourable for the diatoms. However, after some weeks or even months the growth of the diatoms may stop and on careful examination one may find enormous numbers of flagellates of a size of 2–6μ.

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* In my experience only *Rhizosolenia robusta* is liable to be caught by the surface film and has therefore to be transferred very gently.

Before every operation involving the transference of diatoms from one culture dish into another—isolation, washing, subculturing—the pipette should be sterilized by dipping it into boiling glass-distilled water in a beaker and afterwards cooled in sterile culture medium. This is necessary in order to avoid contamination and to clean the pipette.

The cultures were kept at room temperature and placed near a window facing north. During the winter months a 100-w. lamp hanging at a distance of about 1 m. was used to increase the illumination during the day. In summer the cultures of *Coscinodiscus Granii* grew better in a dim light at a distance of 2–3 m. from the north window.

Subcultures were made every two to three weeks and inoculated mostly with 10–100 cells. In spring and summer subcultures of rapidly growing forms like Ditylium, Chaetoceros, Skeletonema and Melosira had to be made at shorter intervals. It is advisable to keep the old cultures for some time because, for reasons mostly unknown, not all subcultures are equally successful. I had several times to return to 4- to 6-weeks old cultures, and then a sample of these old cells was passed at intervals of 1–2 days through a number of watch glasses before inoculating a Petri-dish. Washing the cells to be transferred is also necessary when cultures contain bacteria.

Bacteria-free cultures were not aimed at and no special bacteria tests made. They correspond to Allen's " persistent " cultures, or what are generally called " pure cultures," containing only harmless bacteria besides the one cultured species of protozoa, in contrast to " absolutely pure " or bacteria-free cultures. Since the cultures were frequently examined and a large surface of the watch glasses and Petri-dishes was thus exposed to the air, the occasional appearance of mostly harmless bacteria was to be expected. However, from my experience it seems very probable that with the same methods, but using culture flasks or test tubes instead of Petri-dishes, one could easily get continuous cultures of absolute purity.

It may be mentioned that in January and February, 1936, after having grown extremely well for three months, the cultures of Ditylium gave some trouble by producing numerous cells with slightly contracted and highly refractive protoplasts. The division rate was also very much reduced and it became difficult to make new subcultures. Eventually the difficulties were overcome by adding traces of $CuSO_4$ to the culture medium. The pipette was dipped into a m./10,000 solution of $CuSO_4$ and washed off in the Petri-dish prepared for the subculture. Previously similar traces of Cu were introduced by using for the sterilization of pipettes porcelain-distilled (instead of glass-distilled) water which according to tests made by Dr. L. H. N. Cooper contained definite traces of copper. This might be interpreted as showing that in winter, and probably also in autumn, sea-water contains too little copper, or none at all, which must therefore be added to the culture medium, while in spring there is a sufficient supply of it in sea-water. However, although from January until March many cultures without the addition of $CuSO_4$ were not successful, whereas those supplied with traces of it showed excellent growth, I would hesitate to regard copper as an essential part of the culture medium without more elaborate and controlled experiments. There might have been small numbers of bacteria present the effect of which was checked by $CuSO_4$.

The following diatom species were obtained in pure cultures.*

Biddulphia mobiliensis (Bail.) Grun.
Chaetoceros didymus Ehr.
,, *pseudocrinitus* Ostenfeld
Coscinodiscus excentricus Ehr.
,, *Granii* Gough
,, *radiatus* Ehr.
,, *sub-bulliens* Jörgensen
,, *obscurus* (?)
,, spec.
Ditylium Brightwelli (West)
Melosira Borreri Greville
Rhizosolenia alata Brightw. form *indica* (Péragello)
Skeletonema costatum Greville
Streptotheca thamensis Shrubs.
Thalassiosira spec.

This list includes only those species which were cultured for at least three months through several subcultures—some are now 16 months old.

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* Most of the diatoms cultured were kindly identified by Dr. Marie V. Lebour.

Some others have been cultured for shorter periods and abandoned because there were too many cultures to be cared for. It was, however, reasonably certain that under the conditions given they could have been kept for much longer periods. These species were :

Chaetoceros borealis.
,, *gracilis.*
Eucampia zoodiacum.
Lauderia borealis.
Rhizosolenia Shrubsolei (?).

Cultures of *Biddulphia regia* and *B. sinensis* were not very successful. For short periods of about 4 weeks they divided quite actively. But after that the growth stopped, their shape becoming slightly abnormal and their chromatophores dark brown.

The methods described above were definitely inadequate for *Corethron criophilum* and *Hyalodiscus stelliger.* Although I tried repeatedly, not more than one division took place in isolated Corethron cells and none in Hyalodiscus. The cells of the first species looked extremely healthy the first few days after isolation into " Erdschreiber," being freely suspended in the water, but afterwards the protoplast disintegrated.

THE CULTURING OF OTHER ORGANISMS.

Dinoflagellates.

The culture methods described above were tried out on some plankton dinoflagellates. Only the culture of *Prorocentrum micans* was successful. Two cells were isolated from a plankton sample on September 27th, 1935, and treated in a similar way to the diatoms. They reproduced very quickly and the culture is still in good condition (February, 1937).

Certain other autotroph dinoflagellates, *Ceratium tripos*, *C. fusus*, *C. furca* and *Dinophysis tripos* behaved similarly to Corethron among the diatoms. At first they were much healthier and moved about more actively than in the original plankton sample. One or two divisions took place, with the subsequent separation and restitution of the daughter cells, but no persistent culture could be established, although some cells remained alive for longer than a month. One typical example may be given. On October 4th, 1935, several *Ceratium tripos* were isolated and carefully washed, on the 17th one cell was isolated and washed again. By the 24th it had divided and the two cells were then transferred into fresh medium. On November 5th there were seven cells ; these were washed twice. On the 8th there were only six alive ; they were washed three times. On the 12th six were transferred and of these on the 18th four were alive, which were washed once. On the 22nd only one was alive and very active. This Ceratium was alive on the 23rd and 24th and was transferred each day but by the 30th it had died.

Whatever the reason for the inhibition of their division may have been, it was certainly not caused by the presence of any contaminating organisms, flagellates or bacteria.

Some colourless and probably saprophytic species could be kept alive for some time, *Peridinium depressum* for nearly 4 weeks, and two specimens of *Peridiniopsis* spec. for six weeks. The latter " moulted " after about five weeks, abandoning the old shells and forming new ones, a process which also occurs often in overcrowded cultures of Prorocentrum.

Nannoplankton flagellates.

My attempts to obtain pure cultures of diatoms and dinoflagellates drew my attention to a big and varied group of autotroph nannoplankton flagellates, most of them probably unknown systematically.

If a diatom or a dinoflagellate is picked out from a plankton sample with only a tiny drop of the original medium and transferred into a watch glass with " Erdschreiber," one will almost regularly obtain the growth of one or more species of flagellates rather than that of the diatom or dinoflagellate. If these are passed through one or two watch glasses with sterile medium whereby the original drop of plankton fluid is diluted to 2–4 c.c. one may still obtain a flagellate culture, but it is more likely that it will be a pure culture of one species only. From their presence in diatom cultures started in the way just described it may be concluded that almost every drop of plankton fluid contains one or more flagellates.

By that very indirect method I obtained within several weeks cultures of about a dozen flagellates which were—and some are still—kept in 100 c.c. culture flasks with about 50 c.c. of " Erdschreiber " and subcultured every 3–5 weeks. No special study has been made of them so far. In size they range from less than 2μ to 10μ. The colour of the chromatophores and of the cultures respectively is opaque-green, green, brown and yellow-brown. The movement is characteristic in some species. In one flagellate the periods of movement and of rest, i.e. free suspension in the water, follow each other at varying intervals, the movement starting and stopping with extreme suddenness. Most of the flagellates probably belong to the Chrysophyceae and Cryptophyceae, and a few to the Volvocales.

Once I had gained some experience with regard to their size, shape and movement these tiny flagellates could be found in every sample of townettings examined. Under the binocular, eyepiece ×8, objective ×8, one can see them distinctly down to a size of about 4μ, and under favourable light conditions even those 2μ in size. By the use of the dissecting microscope with its wide field one gets a better, if only a very general, idea of their number and variety than by isolating drops of plankton fluid and examining them under a high power. They appear to be more numerous in spring, summer and autumn than during winter. They were often present in fair numbers in tow-nettings which were extremely poor in diatoms and other phytoplankton. During the autumn and winter of 1935–6 single drops of plankton fluid were occasionally placed in watch glasses with culture medium and invariably gave growth to mostly mixed cultures of flagellates.

The technique of isolating and washing single cells of diatoms cannot be applied to these organisms. It is very difficult to handle objects less than 12μ in size in that way. The isolation is possible, but not the washing in watch glasses because of the difficulty of finding the isolated object again. The dilution method as used by Allen (1910) seemed to be the appropriate one and was tried out with success. One picks out under the binocular what one believes to be a single flagellate—in fact there will probably be two or more specimens in the drop of water drawn into the pipette—and places the drop in 1 c.c. of medium. This is distributed over 5–10 culture flasks and if successful one or the other flask may give a pure culture of a flagellate. If a culture contains two species of flagellates they sometimes will not reproduce at the same rate, but one will have its flowering period after the other. The culture may, for instance, take a more and more intensive golden-yellow colour owing to the growth of one type, then this colour may fade away in a day or two and give way to the green tint of the second flagellate. By repeated subculturing at the right time one can sometimes succeed in gradually separating the two species or eliminating one. The use of solid media would probably give better and quicker results (see Ålvik, 1934).

Some of the flagellates cultured were tried out as food for various larvae. A harpacticid copepod has been cultured for three generations. The adults, about 1 mm. in length, could be fed on flagellates 12μ in size. Newly hatched nauplii died on this diet but lived very well on flagellates of $5–7\mu$. Several polychaete larvae could be observed taking them in, as could plankton copepods. The latter could not be kept longer than 3–4 weeks, but the cause of their death was probably not lack of or inadequacy of food (see p. 765).

All these experiments led me to the conclusion that the autotroph nannoplankton flagellates are of great importance in the food economy of the sea. The bulk of living matter provided by them is probably much smaller than that of diatoms and dinoflagellates, although the proportion in which they appear in tow-nettings certainly is misleading, since flagellates of $2–10\mu$ are not retained in the net to the same extent as the bigger phytoplankton. But their reproduction is more rapid and they are of the right size to be taken in by the filter-feeding organisms, and are far more numerous and more often present in the plankton than small pennate diatoms of the type of *Nitzschia closterium* var. *minutissima*, cultured by Dr. E. J. Allen and successfully used by him and his collaborators in rearing various marine larvae.

Some of the minute algae mentioned above are probably related to or identical with those found in Norwegian oyster pools and investigated by Ålvik (1934). This author obtained pure cultures of six algae which he described as new species. Previous to this work it has been shown by Gaarder (1933) that oysters and their larvae need green algae of 2–3μ as food.

From studies of the plankton of tanks at Conway with enriched sea-water where a good settlement of oyster larvae took place, and of tanks with untreated sea-water where few larvae or none settled, Mr. H. A. Cole (private communication) arrived at a similar conclusion to the Norwegian author (Gaarder, 1933), namely, that nanno-plankton flagellates of a size of 7μ and less are suitable food for oyster larvae.

The whole group of nannoplankton flagellates certainly deserves further investigation along the same lines as those for larger plankton organisms, i.e. systematics, life-history, distribution in the sea, abundance in different seasons, requirements with regard to nutrients, light and other factors governing the life in the sea. An important start has been made by Gaarder (1932), Gaarder and Spärck (1932) and Ålvik (1934) with their studies on Norwegian oyster pools.

Larvae.

To get an idea of the efficiency of "Erdschreiber" as a culture medium larvae were picked out occasionally from the plankton and attempts made to rear them. A Pilidium larva (of a nemertine) was isolated on October 17th, 1935, and transferred every few days into a watch glass with fresh medium and *Chlamydomonas* spec.* as food. This was taken in readily and on November 1st metamorphosis took place. It was very interesting to note that after the release of the young worm the "larva," not much changed in its external appearance, continued swimming about very actively, with the apical sensory hair in slight motion as before. It was alive and active on the 7th but reduced in size and irregular in shape. On the 13th it had disappeared.

On October 1st, 1935, Dr. Allen kindly gave me a Phoronis larva which he had found in a plankton sample. It was placed in "Erdschreiber" with Chlamydomonas as food. The larva started feeding immediately and the algae were driven into the oesophagus and after some time passed into the gut. Here they were kept moving round, towards the oesophagus on the dorsal side, posteriorly on the ventral. After half an hour there were a great number of Chlamydomonas in the gut and its fluid was green. However, the next and the following days very few were taken in and the larva, particularly its tentacles, became gradually reduced in size. The larva remained alive until the 26th.

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* This has been used before as food for *Artemia salina* and *Noctiluca miliaris* (Gross, 1932, 34).

Oikopleura larvae were isolated several times and provided with flagellates of various sizes but always died within 24 hours.

Herring.

The larvae were reared from eggs which had been artificially fertilized* on January 21st, 1936. They hatched on the 31st and on February 1st respectively and 120 larvae were kept in groups of 4—10 in finger-bowls at conditions varied with regard to medium, food and temperature. The following media were tried : " outside " sea-water unsterilized, sterilized by heating to 60°, 70° and 100° C., Allen's modification of Miquel, and " Erdschreiber " with varying amounts of soil-extract. As food were offered : *Chlamydomonas* spec., *Prorocentrum micans*, *Thalassiosira* spec., *Coscinodiscus radiatus* and *Skeletonema costatum*. The cultures were kept at room temperature (reaching 17° C. during the day, dropping to 8–11° at night), on a window-sill on a landing (with a lower day-maximum of about 12–13°) and in containers with running tap water (9–12°).

The yolk sac was absorbed after 6–8 days in all larvae except in those kept under running tap water where most larvae retained it as long as 13 days. Until the yolk sac had gone the mortality was negligible, after that it increased considerably. The majority of the larvae were alive 10 days after the yolk sac had been exhausted, some survived until the 19th–24th at room temperature, and until the 27th in cultures kept under running tap water.

There was no obvious difference in the viability of the larvae kept in different media. Chlamydomonas and Prorocentrum could be seen inside the gut in many larvae soon after the yolk sac had been absorbed, but Thalassiosira only in one larva. The other diatoms were probably too big. Chlamydomonas was sometimes taken in in large masses, so that the gut could be seen as a green line with the naked eye. Some larvae were watched extruding faecal pellets consisting of remnants of Chlamydomonas and to a far lesser extent Prorocentrum.

Lack of food can therefore not have been the cause of their death. That the food offered was inadequate is not likely since Prorocentrum represents an important item of the diet of young herrings (7–12 mm.) in nature (Hardy, 1924). What else could be the reason for the failure in rearing herring larvae ?

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* I am indebted to Mr. E. Ford who performed the artificial fertilization.

Some incidental experiments may be recorded which throw some light on this problem. The larvae—following the ordinary routine in culturing—were transferred to finger-bowls with fresh medium and food every 5–7 days, sometimes at shorter intervals so as to avoid any harmful effects of accumulating metabolic products. However, a very puzzling result was often obtained, the larvae dying a few hours after the transference. At first I thought that they had been damaged by handling them with too narrow pipettes. I then used bigger ones and finally small finger bowls as a kind of spoon with which I transferred the larvae. But the effect remained the same. One instance may be given with more details. A culture of 15 larvae was kept from January 8th till the 13th on the laboratory landing in pure sea-water and all the animals were very healthy during that period. On the 13th seven larvae were taken out with a broad pipette and placed in fresh sea-water from the same bottle as on the 8th. Half an hour later six larvae were lying at the bottom of the bowl, opaque in colour and very weak. Three hours later three larvae were dead, the next day three more, while the last larva fed on Chlamydomonas and survived until the 20th. The herrings which had been left in the old sea-water on the 13th remained very healthy until the 19th when they were cautiously transferred into fresh sea-water+food. Fifteen minutes later four animals were dead, lying at the surface of the water with the body bent abnormally, the brain opaque and the fins broken. A further two larvae died the following day. Similarly several larvae kept under running tap water were killed when transferred into fresh medium.

The explanation may be found in the fact that the stock of sea-water kept in the room was of a temperature several degrees higher than the old medium kept on the landing and under running tap water, and that the sudden change of temperature proved fatal even in such a short time.

Angler-fish.

On March 25th, 1936, a piece of spawn of Lophius was brought in by S.S. *Salpa*. Most of the larvae were hatched and were moving about in the capsules. They were liberated by deliberate cutting with a pair of scissors through the gelatinous ribbon in which they were embedded* and placed in small tanks and finger bowls with the same media as the herrings. Some cultures were kept in an unheated cellar where the temperature varied from 12 to 14·5°, i.e. much less than in the laboratory-rooms, others in a bath with running tap water of a temperature varying between 10·5 and 12°. The yolk sac was absorbed between April 10th and 14th. Prorocentrum, small copepods and cladocera from the plankton and newly hatched nauplii of *Artemia salina* were offered as food. I have only noticed that Artemia nauplii were taken in by the young anglers. On the 15th only three larvae out of 200 kept in the cellar had survived, but 45 out of 150 kept under running water. Of the latter 12 were alive and very lively on the 20th, and 5 on the 21st. They died on the 23rd.

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* If left in it most larvae will hatch out into the water, but an enormous growth of bacteria takes place.

Pilchard.

Larvae of *Sardina pilchardus* were obtained from eggs brought in by S.S. *Salpa* from Station E2 on May 12th. Sixty larvae hatched on the 14th and were kept in the cellar in finger bowls standing in a tank with running tap water. The temperature of the tank water varied from 13·5 to 14·5° C. The media used were sterile sea-water and "Erdschreiber." On the 19th almost all larvae had their yolk sac absorbed; on the 22nd they were seen feeding actively and their guts contained masses of Chlamydomonas and smaller numbers of Prorocentrum. Five larvae were placed in another finger bowl and taken to the main laboratory to show them to some colleagues. They were brought back after about 10 minutes and 20 minutes later 3 were dead and 2 very weak. As the rest of the Pilchards in the original dish were in perfect health the cause for their sudden death could only have been the increase of temperature for 10 minutes.

Discussion.

The preceding account affords an opportunity for discussing the problem why some plankton organisms can be cultured or reared and others not. The methods adopted for culturing diatoms were adequate for quite a number of them. Adding to the list given on pp. 757–58 some more which had been cultured by Allen and Nelson—*Asterionella japonica*, *Chaetoceros densum*, *C. decipiens*, *C. constrictum*, *Cocconeis scutellum*, *Nitzschia closterium*, *N. seriata*, *Rhizosolenia stolterfothi*, to mention only those species not represented on my list—one obtains a very representative selection of most diatom groups present in the plankton off Plymouth. It is all the more peculiar that two species, *Corethron criophilum* and *Hyalodiscus stelliger*, have resisted every attempt to culture them. It appears to me unlikely that these two species should require a medium fundamentally different from that in which there was an excellent growth of the other diatoms all the year round, or that species of Ceratium should need a medium different from that suitable for Prorocentrum and Noctiluca, or an Oikopleura larva a medium different from that of a Pilidium larva. It seems more probable that the temperature of the

Laboratory rooms, being much more variable and altogether higher than that in the sea, is only tolerated by a limited group of species.

The experiments with fish larvae produced good evidence for the assumption that the weakest point of the culture technique used was the lack of controlled and sufficiently low temperature. It has been shown by Lebour (1925) that the critical stage in the life-history of the Angler was not, as might have been expected, directly the yolk sac was absorbed, but a few days afterwards, because for three days the fishes were catching food fast and eating it. In my experiments the Anglers and Herrings survived about 14 days after the yolk sac was absorbed, and the Pilchards 10 days, during which they fed and undoubtedly grew in size. But as the Herrings died 15 minutes after having been transferred into fresh medium of a temperature 1–3° higher than the original medium it cannot be surprising that the rest of them died within 2 weeks or so if exposed to slower but even bigger changes of room temperature. Both Herrings and Anglers kept under running tap water lived a few days longer than at room temperature, although when kept in the cellar the room temperature was considerably steadier than the temperature of the laboratory. The conclusion which may be drawn from these preliminary experiments is that fish-larvae need not only a steady but low temperature. Garstang (1900) concluded from experiments on the rearing of the " Butterfly Blenny " (*Blennius ocellaris*) " that the conditions which are most important for the healthy development of sea-fish larvae, and for the survival of a high percentage of fry through the critical stages of metamorphosis, are the following: (1) A liberal supply of pure water; (2) Mechanical, but moderate, agitation of the water . . . ; (3) Provision of suitable food prior to the absorption of the yolk; and (4) A fairly constant, but not excessive supply of food each day. . . ." Point (4) appears to me of minor importance and low temperature should be included. Under controlled temperature conditions, with supply of the right food for the different stages, one would, I think, stand a fairly good chance of rearing fish larvae. It is one of the improvements of the culture technique which might also lead to a successful breeding of plankton copepods. Crawshay (1915) in experiments on the rearing of plankton copepods showed that temperature is a factor of the greatest importance and that " the daily fluctuations of air temperature to which uncovered vessels are exposed are liable to produce conditions that must sooner or later prove fatal to animals so sensitive to such changes." The best success—rearing of nauplii to the adult stage, with *Nitzschia closterium* as food—he obtained by keeping the culture vessels at a temperature with a varying range of no more than 1·6°, a maximum daily variation of 1°, and an average temperature of 12·3°. Clarke and Gellis (1935) kept copepods at different carefully controlled temperatures with *Nitzschia* *closterium* (from Dr. Allen's culture), Dunaliella, Carteria and Chlamydomonas as food. Under these conditions the majority of the copepods died after about two weeks. But it is possible that those forms were too large since certain experiments " indicate that bacteria and other constituents of the nannoplankton may be an important food for copepods in the sea."

I am grateful to Mr. F. S. Russell, Dr. S. Kemp, F.R.S., and Dr. E. J. Allen, F.R.S., for kindly reading and correcting the manuscript of this paper and giving much helpful advice.

SUMMARY.

The methods are described which made possible the establishment of pure cultures of a number of centric plankton diatoms and of the dinoflagellate *Prorocentrum micans*.

By means of a modified technique cultures were obtained of some nannoplankton autotroph flagellates varying in size from 2 to 10μ. Attention is drawn to their great number in the plankton and to their importance as food in the sea.

Herring, Angler and Pilchard larvae were reared for respectively 27, 29 and 15 days after hatching. The young Herrings and Pilchards fed on *Chlamydomonas* sp. and *Prorocentrum*, the Anglers on nauplii of *Artemia salina*. Some evidence is given for the conclusion that the ultimate failure in rearing these species was caused by too high and variable temperatures.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs. Part I: Some New Observations on Sorting Mechanisms in Certain Lamellibranchs.

By D. Atkins.

Quart. Journ. Micr. Sci., Vol. 79, 1936, *pp.* 181–308.

Accounts are given of the ciliary feeding mechanisms in *Nuculana minuta* (Müller); *Glycymeris glycymeris* (L.) and *Arca tetragona* Poli; *Heteranomia squamula* (L.), *Monia squama* (Gmelin), and *M. patelliformis* (L.); *Pteria hirundo* (L.); and *Solen marginatus* Montagu, *Ensis siliqua* (L.), *E. arcuatus* (Jeffreys), and *Cultellus pellucidus* (Pennant). These Lamellibranchs agree in possessing a certain ciliary sorting mechanism on the gills themselves, namely, adjoining tracts of frontal cilia beating in opposite directions on the same gill filament or leaflet. This occurs in Nuculana on the inner leaflets only; in the Arcidae and Anomiidae (with flat gills) on all filaments; in Pteria, Solen and Ensis (with plicate and heterorhabdic gills) on the ordinary and apical filaments only, and complicated by a difference in the direction of the frontal currents in the plical grooves and on the crests; in Cultellus (with flat gills) on both lamellae of the inner demibranch, but on the ascending lamella only of the outer demibranch.

Tracts of fine frontal cilia, beating continuously, convey particles intended for consumption, while tracts of coarse cilia, fully active only when stimulated, transport material intended to be rejected. In all, except the Protobranch Nuculana, unwanted material is carried to the ventral edges of the demibranchs, which are generally ungrooved or slightly grooved, rarely deeply grooved. In the Arcidae and Anomiidae the current along the edge is posterior in direction, so that such unwanted material as does not fall on the mantle is transported directly to the exterior. In Pteria, Solen, Ensis, and Cultellus the marginal current is oralward, but if the load be heavy much falls on the mantle, and is conveyed posteriorly by its recurrent tracts and finally rejected on sudden closure of the valves.

In the Anomiidae the sorting mechanism on the gills was not observed functioning satisfactorily under experimental conditions, in that there was no appreciable transportation of intended food particles dorsally, and it would seem that members of this family mainly feed on particles brought directly to the broad dorsal food grooves by the water current set up by the lateral cilia.

In Nuculana the highly specialized method of sorting on the small gills seems to have been inherited from a form in which the gills played a considerably greater part in nutrition than they do in this Protobranch, which feeds largely by means of extrusible palp appendages. In *N. minuta* the strength of the inhalent and exhalent currents is augmented at intervals by dorsal contraction of the gills, in which there are striated muscle fibres.

In the Arcidae and Anomiidae the ciliary currents of the visceral mass and mantle are described in detail. In the section on the Anomiidae an Appendix is added on the hypobranchial gland of the genus Monia.

D. A.

Nouvelles Observations sur l'Acétylcholine et la Choline-Estérase chez les Invertébrés.

By Z. M. Bacq.

Arch. Internat. Physiol., Vol. XLIV, 1937, *pp.* 174–189.

The muscles of worms, sipunculi, molluscs and echinoderms are made to contract by acetylcholine. The muscles of sea anemones and crustaceans are insensitive to acetylcholine. Choline-estérase is present in the tissues and fluids of worms, sipunculi, molluscs and echinoderms. It exists in the muscles of the crustaceans, but it does not exist in the blood of the crustaceans or in the muscles of the sea anemones. It is absent from the blood of Arenicola. So far, experiments undertaken in order to demonstrate the existence of cholinergic nerves in Cephalopods have been unsuccessful. Acetylcholine and eserine are without action on the stellate ganglion of Cephalopods.

Z. M. B.

L'" Amphiporine " et la " Némertine " Poisons des Vers Némertiens.

By Z. M. Bacq.

Arch. Internat. Physiol., Vol. XLIV, 1937, *pp.* 190–204.

In the tissues of the nemertean worms Amphiporus and Drepanophorus, there exists an alkaloid " amphiporine " which according to its pharmacological and chemical properties may be classified in the nicotine group.

Amphiporine is not localized in the proboscis of the nemertine and is not, strictly speaking, a venom.

The tissues of most nemertines (particularly in the species Lineus) contain another substance deprived of nicotine-like action, but active at low concentration on the neuro-muscular preparation of the crab.

Z. M. B.

The Development of Isolated Blastomeres of the Ascidian Egg.

By Arthur Cohen and N. J. Berrill.

Journ. Exp. Zool., Vol. LXXIV, 1936, *pp.* 91–117.

Isolated half-blastomeres of *Ascidiella aspersa* produce small tadpoles which possess 0 to 3 papillae, 0 to 2 sense organs, 20 to 22 notochord cells and 19 to 21 muscle cells. The normal tadpole developing from a whole egg possesses 3 papillae, 2 sense organs, 40 to 44 notochord cells and 38 to 40 muscle cells. The first three cleavages of the half-blastomere are strictly partial, but the sliding of the cells as their free surfaces are reduced to a minimum soon masks the characteristic pattern. Explanations are offered to account for the presence of as many as the full complement of papillae and sense organs which would fit both a determinate and regulative conception of the ascidian egg. The presence of partial cleavage and only half the normal number of notochord and muscle cells can only be accounted for on the basis of rigid determination. It is concluded that the eggs of this species should be considered as belonging to the determinate class, although regulation of a type dependent on the action of surface forces occurs.

A. C.

Heterogonic Growth in the Abdomen of *Carcinus maenas*.

By J. H. Day.

Report of the Dove Marine Laboratory (Third Series, No. 3), 1935, pp. 49–59.

From measurements of 560 specimens of *Carcinus maenas*, growth-ratios of individual abdominal segments were determined. These in turn were used to show the growth-gradients along the whole abdomen. While it is realized that these gradients in the abdomen are merely parts of a more general gradient permeating the whole body, it is evident that there is a growth-centre in the third abdominal segment of young individuals of both sexes. Mature crabs have a growth-centre in the sixth segment. The balance of evidence is in favour of the separate origin of the two growth-centres, rather than a gradual movement along the abdomen.

There is also evidence that the appearance and increasing influence of the growth-centre in the sixth segment is correlated with sexual development and in this connexion it is interesting to note that at the onset of sexual maturity there is a rise in growth-potential in the female and a fall in the male.

It is believed that this is the first recorded case of an organ, the abdomen, passing from the influence of one growth-gradient to another, the second of which is correlated with sexual development. J. H. D.

Observations on the Sporozoa Inhabiting the Gut of the Polychaete Worm *Polydora flava* Claparède.

By R. Ralph Fowell.

Parasitology, Vol. XXVIII, 1936, *pp.* 414–430.

Polychaete worms harbour some very characteristic Sporozoa; and *Polydora flava* is certainly no exception to the rule. A Coccidian—which is clearly an Eimeriid—is, perhaps, the most interesting parasite of Polydora owing to its striking resemblance to the Coccidia of higher animals; and it is also remarkable in being an intranuclear parasite. Unfortunately, the fate of the undivided contents of the oocyst is unknown.

The other parasites of *Polydora flava* include a dicystid gregarine, *Polyrhabdina polydorae*, and a schizogregarine, *Selenidium axiferens* n. sp.; this organism possesses a remarkable axial tube which extends from one end of the body to the other and completely encloses the nucleus. The axial tube forms an integral part of the fibrillar complex, being connected, by whorls of radial fibrils spaced at regular intervals along the body, with a superficial system of longitudinal myonemes underlying the pellicular grooves. Schizogony and stages in sporogony, up to the formation of isogametes, are described; and association in *Polyrhabdina polydorae* is recorded for the first time. R. R. F.

Neuro-muscular Transmission in Crabs.

By Bernhard Katz.

Journal of Physiology, 1936, *Vol.* 86, *pp.* 45–46 P. *and Vol.* 87, *pp.* 199–221.

The electric excitability and the effect of different pharmacological agents on the neuro-muscular system of *Carcinus maenas* were investigated. The mechanical response of the flexor muscle of the dactylopodite in isolated walking legs, and the electric response of nerve and muscle were recorded. Visible muscle contraction, during indirect stimulation, results from repetitive nerve excitation only. The majority of muscle fibres come into action at frequencies of 60–120 per sec. (20° C.). The gradation of the muscle response is controlled by the number of "facilitated" nerve endings, increasing statistically with frequency. The time constant k (Hill) in nerve excitation, determined from strength-duration curves (repetitive condenser discharges) for electric response of the nerve, or for threshold contraction of the muscle, is about 1 msec. at 20° C. The limb nerve gives prolonged multiple response to constant current both at make and break, due to its very slow accommodation process. The frequency of impulses varies with intensity of applied current up to an upper limit (about 300 per sec. at 20° C.), determined by the absolute refractory period. Calcium, in about fifteen times normal blood concentration, quickening the accommodation process, abolishes reversibly the multiple response. The nature of neuro-muscular transmission is investigated. Curare, acetylcholine and eserine have little or no effect on the neuro-muscular junction. Potassium applied to the neuro-muscular junction causes contracture, even in three times normal concentration. The initial part of the contracture is of a tetanic nature, being accompanied by rhythmic electric response. Magnesium, even in 2·5 times normal blood concentration, has a reversible curare-like blocking effect on the myoneural junction, and acts as an antagonist to potassium in respect of contracture. The electric response of the nerve is abolished by potassium, increased by magnesium, in about the same concentrations as those effective on the nerve endings.

B. K.

Observations and Experiments on Sex-change in the European Oyster. V. A Simultaneous Study of Spawning in 1927 in Two Distinct Geographical Localities.

By J. H. Orton.

Mélanges Paul Pelseneer, Mémoires Mus. Roy. Hist. Nat. Belg., Ser. 2, *Fasc.* 3, *pp.* 997–1056.

In this study some 10,000 oysters from the Fal Estuary and some 5,000 from the River Blackwater were examined during and about the spawning season in 1927, giving mostly large weekly samples. An analysis for sex-proportions and spawning confirms and establishes the fact that on English beds at least 50% of the population above the age of three years mature annually as ripe females, mostly near the beginning of the spawning season, and become gradually expended as they spawn during the season. Spawning began at different dates on both beds when the sea-temperature attained about 15° C.; a correlated study of seasonal variation in sea-temperature is given. Fluctuation in weekly percentage of premature and normal whitesick, greysick and blacksick are noted with their bearing on oyster-culture, and periods of development of larvae *in situ* in the parent in the sea are adduced from the results. The factors contributing to the spawning stimulus, the effect of temperature and salinity fluctuation on spawning, the theory of the time-calorie period of development in relation to spawning and other problems are discussed.

The female population on the Blackwater was exhausted to a minimum of 3% in August, whereas 20% of the population on the Fal were unexpended at the same time and failed to spawn effectively. A discussion of the phenomena and probable controlling factors is given. A study of the gross proportion of the population acquiring femaleness (including assumptions of the hermaphrodite phase) during the season, and of other problems, is being continued from the data obtained.

J. H. O.

The Photo-electric Measurement of Submarine Illumination in Off-shore Waters.

By H. H. Poole.

Rapp. and Proc. Verb. Cons. Internat. p. l'Explor. de la Mer., CI, 2e Partie, 12 pp.

Photo-electric cells of the selenium rectifier type appear to be the most suitable at present available for the measurement of submarine daylight.

As a low-resistance circuit is essential for measurements in bright light, and it is difficult to combine this with adequate sensitivity in a galvanometer suitable for use at sea, the modified Campbell Freeth potentiometer circuit has been made use of. This combines zero effective resistance with a sensitivity extending to 10^{-9} ampère, and is virtually unaffected by the rolling of the ship.

A brief description is given of the marine equipment which has been found to be suitable.

The optical conditions affecting a submerged photometer are considered, and the need is pointed out for a suitable opal diffusing window in contact with the water. Notes are given of the colour filters used for isolating different parts of the spectrum.

Depth errors due to the drift of the ship must be guarded against, and the error due to shading reduced as far as possible by suspending the photometer from a spar projecting over the stern. The length of the spar is generally limited by motives of convenience, and by the extent of the ship's pitching motion.

The accuracy obtainable under water varies greatly according to the weather. As, however, the illumination generally falls by from 10 to 20 per cent per metre (or much more for red light) depth errors are likely to be as important as photometric errors.

The vertical extinction co-efficient found from the ratio of the illuminations at two different depths is a convenient index of the opacity of the water, although Pettersson's direct method of comparison of the opacities of different waters possesses some important advantages.

H. H. P.

The Effect of Parasitism by Larval Trematodes on the Tissues of *Littorina littorea* (Linné).

By W. J. Rees.

Proc. Zool. Soc., London, 1936, *pp.* 357–368, *Plates I–IV*.

The effects produced by the following larval trematodes were studied : *Cercaria Himasthla secunda* (Nicoll), *C. littorinae* Rees, *C. lophocerca* Lebour, *C. emasculans* Pelseneer and an ubiquitous cercaria (near *C. ubiquitoides* Stunkard). The total percentage infestation varied considerably depending on local conditions, including the distribution and habits of the final hosts of these larvae.

Differences in the parasitization of the digestive gland and gonad by the different parthenitae were found to be due to three factors which are interdependent : 1. The nature of the parthenita, whether sporocyst or redia. 2. The size of the individual parthenitae. 3. The presence of a " blocking layer " formed by inactive sporocysts.

W. J. R.

An Investigation of the Post-Larval Development of the Shore Crab, *Carcinus maenas*, with Special Reference to the External Secondary Sexual Characters.

By C. J. Shen.

Proc. Zool. Soc., London, 1935, *pp.* 1–33, 28 *figs*.

The male and female crabs can be distinguished not only in the adult stage, but also in early post-larval stages, by means of the following three external sexual characters : (*a*) the pleopods, (*b*) the abdomen, and (*c*) the carapace.

The first character alone is diagnostic for all crabs ; the second and third ones are applicable only within limits.

(*a*) *The pleopods* of the megalopa and first young crab stages do not show any remarkable sexual characters except a slight difference in size, but the sexes can be readily distinguished by means of the pleopods at the second young crab stage.

(*b*) *The abdomen:* The form of abdomen can be distinguished between the two sexes at about the fifth young crab stage.

(*c*) *The carapace:* The form of carapace in early post-larval stages exhibits no significant sexual differences. The growth-rate, however, is rather higher in the female as compared with the male from the fifth young crab stage onwards.

C. J. S.

New Species of Zostera from Britain.

By T. G. Tutin.

Journ. Bot., Aug., 1936, *pp.* 227–230.

A new species of Zostera belonging to section Alega was noticed during an investigation into the causes of the disease of *Z. marina* L. and named *Z. Hornemanniana*. It differs from *Z. marina* which is its closest ally in the narrow leaves, rounded or emarginate at the apex, with three primary and two marginal nerves, much smaller flowers and inflorescences, and in having the style twice as long as the stigmas and seeds only 2·5 mm. long. It appears to be fairly common round the coasts of the British Isles and Western Europe and occupies a distinct ecological niche. It usually occurs on soft mud in estuaries at rather high levels, though in one locality it grows permanently submerged. It keeps its distinctive characters in cultivation and is readily recognizable in the field, though herbarium specimens often present difficulties to the systematist. The chromosome number is twelve, the same as in the other two British species, the chromosomes closely resembling in size those of *Z. marina*. The plant is quite fertile and shows no evidence of hybrid origin.

T. G. T.

The Development of the Sabellid *Branchiomma vesiculosum*.

By Douglas P. Wilson.

Quart. Jour. Micro. Sci., Vol. 78, 1936, *pp.* 543–603.

The Sabellidae are a large and widely distributed family of Polychaetes whose mode of development is almost entirely unknown. In this paper the embryology of the well-known species *Branchiomma vesiculosum* Montagu is described in detail and illustrated for the first time. The larvae were obtained from artificial fertilizations and were reared through metamorphosis and for some time afterwards. The larvae are well provided with yolk and do not feed during their pelagic life, which lasts only eight or nine days. They have a prototroch, but no telotroch. In the last swimming stages the primary buds of the branchial apparatus arise on the head in front of the prototroch; the collar buds appear behind the prototroch. During metamorphosis tissues of the prototroch and larval parts of the head clump together to form a snout-like structure that gradually breaks up into pieces which are discarded. The young worm secretes a tube of mucus for itself on the bottom and later builds one with sand grains.

At metamorphosis there are generally three or four chaetigers of thoracic type already formed; afterwards thoracic chaetigers are added in front of the pygidium until the adult number of eight has been attained. Succeeding segments are all abdominal in type. There is no change over from abdominal to thoracic constitution during normal development as has been reported for Serpulids, or as occurs in adult Sabellids during certain types of regeneration.

The early larvae of *Sabella pavonina* (Savigny) are shown to resemble closely those of Branchiomma.

D. P. W.

Observations on Pigmentary Co-ordination in Elasmobranchs.

By U. M. Wykes.

Journ. Exp. Biol., Vol. XIII, 1936, *pp.* 460–466.

Hogben's recent study of the pigmentary system of English Elasmobranchs showed that the colour responses of these fishes are under the control of two pituitary hormones. The experiments of Parker on Mustelus, however, have led him to conclude that in this fish melanophore contraction is brought about by nervous impulses.

The possibility of nervous control of pigmentary responses was investigated in *Raia brachyura*, *R. maculata*, *Rhina squatina*, and *Scyllium canicula*. No melanophore changes could be observed either macro- or microscopically after section of four consecutive spinal nerves in black or white adapted specimens, nor after electrical stimulation of spinal nerves, the haemal canal, or skin. Adrenalin, while having no effect on excised skin, was found to cause slight general pallor on subcutaneous injection. Possibly adrenalin injections affect the colour indirectly as a result of vaso-constrictor action. When the circulation in the tail and pelvic fins was impeded by an aortal ligature, melanophore changes were temporarily eliminated in these regions, though they could still be induced in the rest of the body.

These experiments suggest that, in the species investigated, the nerves play no part whatever in the control of background responses, which are under the exclusive influence of circulatory hormones.

U. M. W.

The Structure of Nerve Fibres in Sepia.

By J. Z. Young.

Journ. Physiol., Vol. LXXXIII, 1934, *pp.* 27–28 *P.*

The peripheral nerves of Decapod Cephalopods contain very large axons, those of Loligo approaching 1 mm. in diameter. These, as well as the smaller axons, are surrounded by nucleated sheaths. The substance of the axon is semi-fluid, and when the larger axons are cut their contents pour out from the end of the tube. A faint longitudinal striation is visible in the axon of the living nerve fibres, but there are no neurofibrils which can be followed for long distances.

J. Z. Y.

The Giant Nerve Fibres and Epistellar Body of Cephalopods.

By J. Z. Young.

Quart. Journ. Micr. Sci., Vol. LXXVIII, 1936, *pp.* 367–386.

In Decapod Cephalopods there is a system of giant nerve fibres which probably serve to produce rapid contractions of the muscles of the mantle. In Loligo the giant fibres in the stellar nerves arise in a special giant fibre lobe of the stellate ganglion, and they are syncytia, each being formed by fusion of the processes of a large number of nerve cells.

In Octopods there are no giant fibres, but in the position of the giant fibre lobe there is a small closed vesicle, coloured yellow in some species, to which the name " epistellar body " is given. The walls of this vesicle contain curious cells, the neurosecretory cells, whose general structure resembles that of neurons, but whose processes (axons) end blindly embedded in a homogeneous non-cellular matrix which fills the cavity of the epistellar body.

After removal of both epistellar bodies from *Eledone moschata* the animal shows general muscular weakness, which lasts for some days. It is suggested that the epistellar body has arisen in phylogeny from the giant fibre lobe and that the neurosecretory cells produce at their inner ends a hormone which passes into the blood stream.

J. Z. Y.

The Innervation and Reactions to Drugs of the Viscera of Teleostean Fish.

By J. Z. Young.

Proc. Roy. Soc., London, B., Vol. 120, 1936, *pp.* 303–318.

Faradic stimulation of the vagus nerve of Lophius or Uranoscopus is followed by movements of the stomach, whereas stimulation of the splanchnic nerve causes movements of the pyloric caeca and intestine.

There are no other motor nerves to the intestine other than those contained in the single pair of splanchnic nerves. Acetylcholine was found to cause a rise of tonus and initiation of rhythmic contractions in the muscles of the stomach, intestine, rectum and gall bladder, whereas adrenaline produced the reverse effects.

The walls of the ovary and urinary bladder receive motor fibres from the abdominal sympathetic ganglia, and these muscles are also usually caused to contract by acetylcholine and are inhibited by adrenaline. These results make it very difficult to draw any clear line between sympathetic and parasympathetic systems in fishes, and in particular they show that there is nothing corresponding to the sacral parasympathetic system of Mammals.

J. Z. Y.

The Structure of Nerve Fibres in Cephalopods and Crustacea.

By J. Z. Young.

Proc. Roy. Soc., London, B, Vol. 121, 1936, *pp.* 319–336.

The sheaths around the axons of Cephalopods are nucleated throughout, and the tissue of which they are composed resembles collagenous connective tissue. The axons may be nearly 1 mm. in diameter and each consists of a rather viscous fluid apt to flow out of the sheath if the latter be damaged. No definite neurofibrils traceable for long distances are present in the axoplasm, but there is a faint longitudinal striation which is visible during life and becomes much more definite if the axon be damaged in any way, presumably on account of the coagulation of longitudinally orientated micelles. It is estimated that 65–70% of the cross-sectional area of Cephalopod nerves is occupied by the axoplasm.

In the leg nerves of Maia each axon is surrounded by a continuous sheath, whose nuclei extend even to the innermost layers. There is some fat present, especially in the inner layers. The sheaths around the larger axons of Maia are very thick, consisting of many concentric layers. 60–70% of the cross-sectional area of the leg nerves of Maia is occupied by axoplasm.

J. Z. Y.

Book Notice.

Color Changes of Animals in Relation to Nervous Activity. By G. H. Parker. University of Pennsylvania Press, 1936. London: Humphrey Milford: Oxford University Press, IX+74 p. 7/-.

The apparent paradox that the colour changes of teleostean fishes and reptiles are controlled by nerves, while those of amphibia are controlled by hormones has long been a barrier to the formulation of a consistent theory of colour response in vertebrates. Professor G. H. Parker has arrived, on the basis of numerous experimental investigations by himself and his collaborators, at a new interpretation which claims to overcome this difficulty. The interpretation is presented in the Leidy Memorial Lectures which are published in the book under review.

That the activation of melanophores is effected through the mediation of a chemical substance, a neurohumour, which is liberated at the chromatophoral nerve endings, is a conception which gains strong support from recent discoveries of chemical agents in nervous transmission. But the interpretation of the experimental data in terms of a neurohumoral mechanism has led Professor Parker to postulate a principle which many physiologists will find it hard to accept, especially as it is supported, at best, by indirect evidence. This principle is that when chromatophoral nerves are cut "they are not at once paralysed, as was formerly thought, but they are by the very act of cutting thrown into a state of superactivity which may last in *Fundulus* for two, three, or more days."

The whole of Professor Parker's theory of the control of pigmentary activity must stand or fall by the validity of this new conception. That it is unorthodox does not mean that it is untrue, but, since physiological methods exist to-day which are capable of subjecting it to a conclusive test, Professor Parker's case must remain *sub judice* until such tests have been applied.

At the same time it has to be admitted that no other interpretation has ever been put forward to account for some of the phenomena, like the paling of dark bands after nerve section, with which Professor Parker deals. A working hypothesis is far better than no hypothesis at all, and Professor Parker has made a contribution of first importance to the subject by drawing attention to many new phenomena that have hitherto been overlooked, and by advancing a theory that will undoubtedly stimulate much further work and discussion.

A. Sand.

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